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Application of an acoustic–trawl survey design to improve estimates of rockfish biomass

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Abstract—Biomass estimates of several species of Alaskan rockfishes exhibit large interannual variations. Because rockfishes are long lived and relatively slow growing, large, short-term shifts in population abundance are not likely. We attribute the variations in biomass estimates to the high variability in the spatial distribution of rockfishes that is not well accounted for by the survey design currently used. We evaluated the performance of an experimental survey design, the Trawl and Acoustic Presence/Absence Survey (TAPAS), to reduce the variability in estimated biomass for Pacific ocean perch (*Sebastes alutus*). Analysis of archived acoustic backscatter data produced an acoustic threshold for delineating potential areas of high ("patch") and low ("background") catch per unit of effort (CPUE) in real time. In 2009, we conducted a 12-day TAPAS near Yakutat, Alaska. We completed 59 trawls at 19 patch stations and 40 background stations. The design performed well logistically, and Pacific ocean perch (POP) accounted for 55% of the 31 metric tons (t) of the catch from this survey. The resulting estimates of rockfish biomass were slightly less precise than estimates from simple random sampling. This difference in precision was due to the weak relationship of CPUE to mean volume backscattering and the relatively low variability of POP CPUE encountered. When the data were re-analyzed with a higher acoustic threshold than the one used in the field study, performance was slightly better with this revised design than with the original field design. The TAPAS design could be made more effective by establishing a stronger link between acoustic backscatter and CPUE and by deriving an acoustic threshold that allows better identification of backscatter as that from the target species.

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Typically, surveys of resource biomass are designed around simple random sampling (SRS), stratified simple random sampling (SSRS), or systematic sampling (Thompson, 2002). One of these standard designs will perform adequately when the resource is relatively uniformly distributed or when the areas where variability in biomass is highest are static and well known. In practice, many resources, such as fish populations, exhibit highly variable and complex spatial structure, and standard survey methods lead to extremely imprecise estimates of biomass (Hanselman and Quinn, 2004). Novel sampling designs have been developed to improve abundance estimation under these circumstances. One example is adaptive cluster sampling (ACS; Thompson, 1990; Thompson and Seber, 1996), which has been explored both in the field (e.g., Lo et al., 1997; Woodby, 1998; Conners and Schwager, 2002; Hanselman et al., 2003) and in simulation studies (Christman, 1997; Brown, 1999; Christman and Pontius, 2000; Christman and Lan, 2001; Brown, 2003; Su and Quinn, 2003). Other methods have been used: double sampling, ratio, and regression estimator approaches to improve precision (Eberhardt and Simmons, 1987; Hanselman and Quinn, 2004; Fujioka et al., 2007). These approaches improve precision by relating a variable that is expensive or difficult to collect (e.g., trawl catches) to a correlated auxiliary variable of which many samples can be collected quickly or inexpensively (e.g., acoustic data).

A resource for which standard survey methods have proven inadequate, Alaskan rockfishes (*Sebastes* spp.) are abundant and supported a valuable commercial trawl fishery with an average exvessel value of US$ 15 million between 2008 and 2010. Survey estimates of biomass for many Alaskan rockfish species exhibit large interannual variations that are not consistent with the longevity (>80 years) and relatively low productivity of these species (Hanselman et al., 2003; Fig. 1). One of the causes of imprecision in survey estimates of biomass is the high variability in the spatial distributions of rockfish populations. For example, the biomass estimate of Pacific ocean perch (*Sebastes alutus*) from the survey con-

ducted in 1999 was driven by several very large catches, out of >800 trawls, that resulted in extremely imprecise estimates (Fig. 1). In addition to having variable spatial distributions, some rockfish species have an affinity for rocky habitat, school semipelagically, and use different habitat types by size class (Stanley et al., 2000; Zimmermann, 2003; Rooper et al., 2010). These factors contribute to high sampling variability and demonstrate the need for examining alternative sampling designs or other technologies to improve survey estimates of biomass (Godø, 2009).

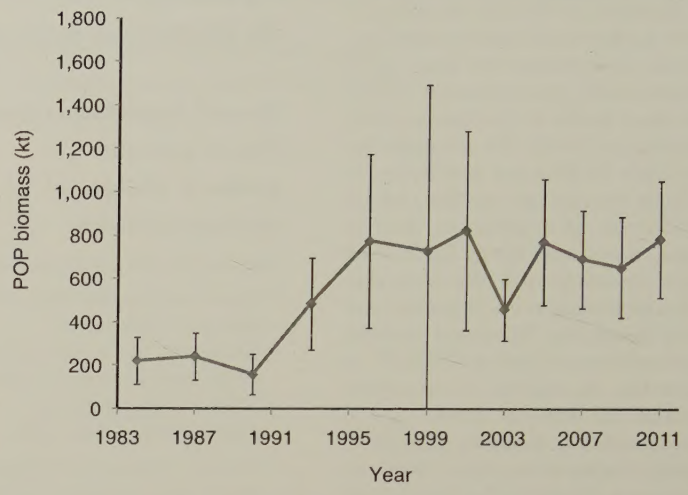

Figure 1

Biomass estimates, shown in kilotons (kt), for Pacific ocean perch (*Sebastes alutus*, POP) determined from National Marine Fisheries Service groundfish trawl surveys conducted in the Gulf of Alaska. Error bars are approximate 95% confidence intervals.

The difficulty of surveying rockfish populations has been studied by using traditional survey designs like SSRS for some time (e.g., Lenarz and Adams, 1980). More recently, several attempts to improve survey precision for Alaskan rockfish species have been made by using alternative sampling designs. The utility of ACS has been examined in several studies (Hanselman et al., 2001; 2003). Many recent attempts have been made to use concurrently collected acoustic data to improve abundance estimation for demersal species (Ona et al.[1]; Hanselman and Quinn, 2004; McQuinn et al., 2005; Fujioka et al., 2007). This subject also was the focus of a European-Union–funded project (combining acoustic and trawl surveys to estimate fish abundance, CATEFA; Hjellvik et al., 2007). These studies showed improvements in survey precision with the use of various measures, including accuracy and travel costs, but none of the survey designs were much more precise than that of a design that was stratified optimally for a particular species. For Pacific ocean perch (POP) in the Gulf of Alaska (GOA), Krieger et al. (2001) showed a relatively strong relationship between catch rates and raw acoustic backscatter in a small study area. Acoustic data were collected sporadically during the NMFS GOA trawl surveys between 2001 and 2004 (Hanselman and Quinn, 2004) and have been collected consistently from 2005 to the current study (2012). Several studies have correlated these acoustic data with trawl catch for rockfishes (Hanselman and Quinn, 2004; Fujioka et al., 2007) and walleye pollock (*Theragra chalcogramma*) (von Szalay et al., 2007). Although much of the previous research has focused on combining results from trawl surveys and acoustic surveys into a single biomass estimate by assessing their relative catchabilities, the focus of our study was to attempt to use acoustic data to improve a traditional trawl survey design.

Our objective was to test the hypothesis that the use of acoustic data in real time in the field to delineate areas with higher trawl-survey catch per unit effort (CPUE) of POP, relative to other survey areas, could increase precision of biomass estimates from trawl surveys. To test this hypothesis, we employed an experimental sampling design, the Trawl and Acoustic Presence/Absence Survey (TAPAS) (Everson et al., 1996). This design is a variant of the double sampling design (Thompson, 2002) and acoustic backscatter data are used to estimate the presence and size of areas, or "patches," where CPUE may be high, compared with other survey areas, and to estimate the proportion of the total area classified as patches. Trawls are conducted at stations randomly selected before a cruise (planned stations) and in the acoustically detected high-CPUE patches identified during a cruise. The rationale of this design is to reduce sampling variability by allocating more sampling effort in the areas of higher CPUE. If high-CPUE areas can be correctly identified with acoustic backscatter, it should be possible to estimate biomass more efficiently. As with other double sampling designs, a critical assumption is that the auxiliary variable (e.g., acoustic backscatter) shows a strong correlation with the primary variable (e.g., trawl CPUE). We believe our study describes the first field application of this TAPAS design.

Materials and methods

Field methods

The study area for our 2009 field experiment was chosen because we had prior CPUE and acoustic data from the NMFS GOA trawl surveys and CPUE data from a prior ACS experiment (Hanselman et al., 2003). We confined

[1] Ona, E., M. Pennington, and J. H. Vølstad. 1991. Using acoustics to improve the precision of bottom-trawl indices of abundance. ICES Council Meeting (CM) document, 1991/D:13, 11 p.

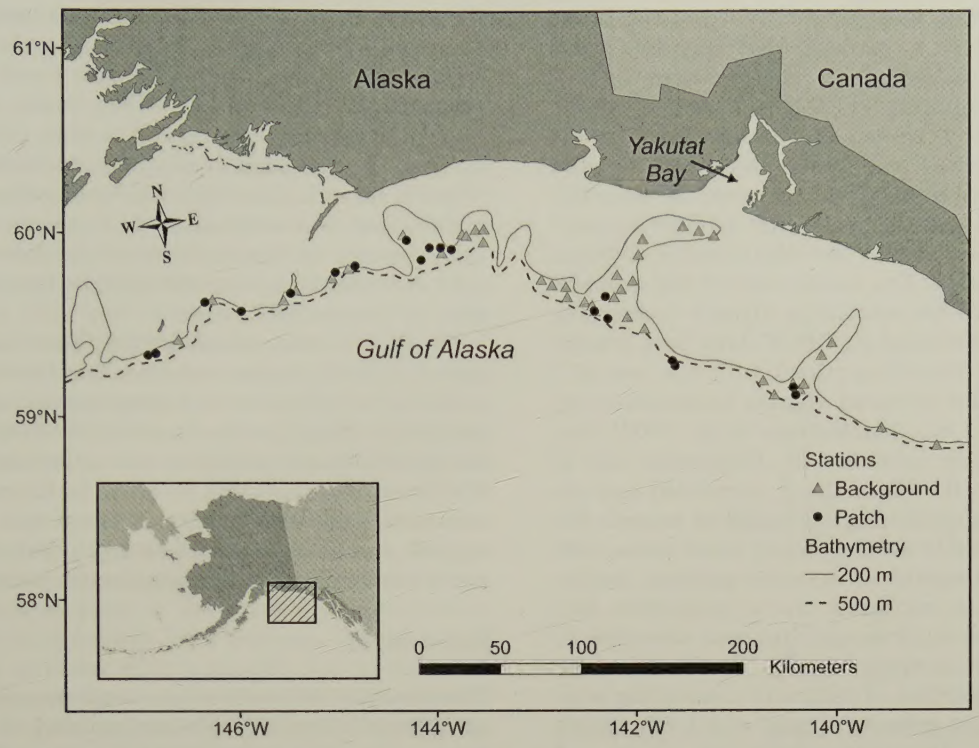

Figure 2

Stations sampled during an experimental rockfish acoustic–trawl survey conducted in 2009 near Yakutat, Alaska, at depths of 200–500 m. Gray triangles indicate "background" stations, which were areas of low-density catch per unit of effort (CPUE) identified in the field through the use of acoustic data. Black circles indicate "patch" stations, which were areas of high CPUE identified in the field.

our study area to the NMFS-delineated strata on the continental shelf break at depths of 200–500 m in the Yakutat area of the GOA (Fig. 2) because these depths contain the bulk of POP biomass. The sampling area was 7800 km^2.

The vessel used for our 2009 study was the FV *Sea Storm*, a 38-m stern ramp trawler with 1710 continuous horsepower. Stations were sampled with a standardized Poly-Nor'eastern high-opening bottom trawl rigged with roller gear and a 27.2-m headrope. All gear was the standard gear used for the NMFS GOA trawl surveys. For further details on the vessel and gear used for our 2009 study, see the report by von Szalay et al. (2010). Acoustic backscatter was measured continuously during the day and during trawling, with a calibrated Simrad[2] (Kongsberg Maritime AS, Horten, Norway) ES60 echosounder and a hull-mounted 38-kHz transducer. A total of 48 stations were preselected randomly from among stations that were successfully trawled during previous NMFS GOA trawl surveys (Fig. 2). The use of previously trawled locations eliminated search time for new locations suitable for random trawls. Once random stations were selected, we constructed the most efficient path, or trackline, to connect these planned stations. Depending on the acoustic backscatter encountered during a survey, these planned stations were later classified as either "background stations" (with low CPUE) or "patch stations" (with high CPUE).

The identification of patch stations required a simple and consistent definition for the spatial variability in acoustic backscatter along the trackline so that we could determine areas of intense backscatter that were large enough for bottom trawling. Acoustic backscatter data were examined in real time by using the Echoview live viewing module (Myriax Pty., Ltd., Hobart, Australia), and Echoview scripts were used to integrate the acoustic backscatter in cells along the seafloor. The conformal cells in this analysis had a height of 10 m (from 1.5 m to 11.5 m off the seafloor) and a length of 100 m. The lower boundary of each cell was situated 1.5 m off the seafloor to avoid errors in Echoview-derived bottom detection and to account for the "acoustic dead zone" (Simmonds and MacLennan, 2005)—the area where fishes are difficult to detect acoustically because the echo from the seafloor masks their acoustic signals. The value of 1.5 m was estimated with the equations in Ona and Mitson (1996) and a peak POP depth of ~225 m (Hanselman et al., 2001). The 10-m height of the cells examined in our study was considerably larger than the mean height (~6 m) of the nets used in NMFS

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

bottom trawl surveys, but this difference accounts for POP swimming above a trawl net that may dive down into the net path in response to the pressure wave of the trawl. This potential for "herding" may increase the effective height of the net. In addition, Aglen (1996) found that the correlation between catch and acoustic backscatter off the seafloor was greatest for Atlantic species of *Sebastes* and suggested that a taller acoustic layer should be more robust for identification of areas of intense backscatter. The actual size of the acoustic layer, however, does not contribute directly to biomass estimates, which are based on CPUE data from trawls.

Patch definition was determined with the use of 2 metrics: 1) the value of mean volume backscattering, S_v (log decibels re 1 m^{-1}; MacLennan et al., 2002) that defines high acoustic intensity (S_v threshold) and 2) the proportion of cells where the S_v threshold was exceeded. A proportion criterion was used to smooth the S_v values across cells to avoid defining small areas with high acoustic backscatter as discrete patches. Analysis of archived data indicated that a proportion was preferable to a moving average that was sensitive to intermittent large increases in S_v. The distance for evaluating the proportion of cells was a sampling window that spanned 31 cells for a total of 3.1 km, which is comparable to the distance needed to prepare for and conduct a bottom trawl. For our study, an area became designated as a patch when the proportion of cells in the sampling window that exceeded an S_v of −65.6 dB was 0.39 or higher. The criteria for patch definition were determined by using the 80th percentile of values from acoustic backscatter data measured aboard the FV *Sea Storm* during a NMFS GOA trawl survey in 2005 in the same Yakutat area. The acoustic backscatter data were echo-integrated in Echoview, and the S_v values were exported and analyzed with R software scripts, vers. 2.9.0 (R Development Core Team, 2009), which generated graphs showing values of S_v that defined the start and end of patches meeting the threshold criteria (Fig. 3). In each identified patch, a location for a patch station that was at least 1 km (a single trawl length) from the edge of that patch was randomly selected, and a 10-min trawl was conducted from that random location as the starting point.

The CPUE data collected from these trawls were assigned to patch stations (random trawls conducted within identified patches) or background stations (trawls conducted within planned stations at which the acoustic threshold was not exceeded). It is important to note that if a planned station was found to be located within an acoustically identified patch, a trawl was conducted at a patch station that was randomly selected within that patch rather than at the preselected location.

Data analysis

The acoustic backscatter data were processed and then categorized according to vessel activity. Echoview software was used to correct the backscatter data for noise and erroneous seafloor tracking. Partitioning backscatter by vessel activity was necessary to accurately estimate the size of patches and the total length of the path traveled by the FV *Sea Storm* inside patches. Hence, to eliminate double counting, we avoided trackline segments where the boat circled around to set up trawls or searched for ground suitable for trawls. Seven vessel-activity categories were assigned to each 100-m cell: 1) transiting between stations, 2) returning to set up a trawl, 3) searching for ground suitable for trawls, 4) trawl deployment, 5) trawling (with offset for trawl distance behind the vessel), 6) trawl recovery, and 7) other transit that was not part of our study. Categories 1 and 4–6 were included in this study. Overlap, defined as anywhere the vessel path was within 50 m of the haul or earlier vessel path, was measured with ArcGIS software (ESRI, Redlands, CA, vers. 9.2).

CPUE was an estimate of fish density (kg/km^2) at each station and was calculated as the catch of a species in kilograms divided by the area sampled (i.e., the product of the net width in kilometers and the trawl trackline in kilometers). Patch length was computed with the haversine formula to calculate great-circle distances (as implemented in the R package argosfilter; R Development Core Team. 2009) between GPS coordinates for

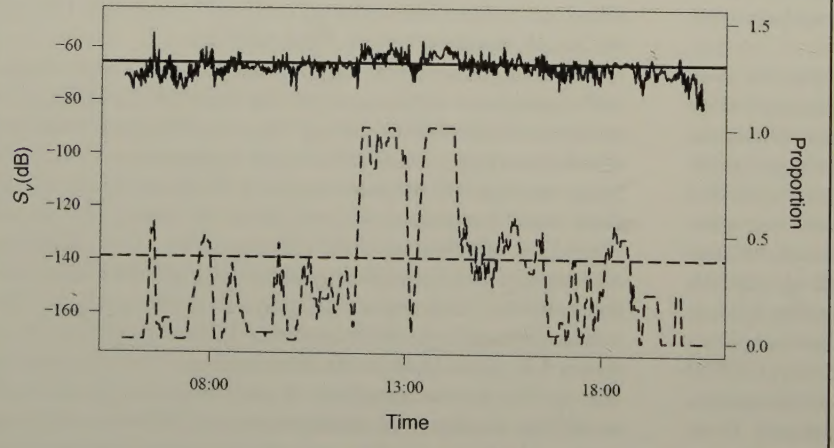

Figure 3

Example of script outputs for real-time monitoring of patches during a 2009 acoustic–trawl survey. The time series (solid wavy line) and solid horizontal line represent mean volume backscattering (S_v) per 100 m and S_v threshold, respectively. The dashed time series and horizontal lines represent the proportion of 100-m cells exceeding the S_v threshold over a 3.1-km window and the threshold for the proportion, respectively. Time is given in Alaska Daylight Time.

every 100-m interval. These calculations were compared with results from summing the number of cells to verify that all cells were very close to 100 m in length and that the GPS systems functioned correctly. For example, using the GPS coordinates, we checked that a 10-cell window in Echoview was ~1 km in length.

We computed biomass estimates with 2 types of methods to compare magnitude and precision. With the first method, we omitted the patch stations, except when a patch station was originally a planned station, and calculated the abundance with an SRS estimator with the sample size used as if the full number of trawls had been sampled by simple random sampling (Thompson, 2002). For the second method, we used the estimator derived for the TAPAS design. The TAPAS estimator is functionally similar to an SSRS estimator, with an important exception: in the TAPAS estimator, CPUE values from patch stations are treated as multiple strata weighted by their associated patch size, but, in an SSRS estimator, only the total area estimated to be in the patch stratum is used. An SSRS estimator was not used in our study for 2 reasons: 1) each patch is a separate stratum with a sample size of one, and therefore within-strata variances cannot be computed and 2) the sampling design introduces patch length as an additional random variable that may or may not correlate with CPUE. If there is no correlation with patch length and CPUE, and the relationship between S_v and CPUE is weak, then using the TAPAS design is similar to suboptimally allocating samples in an SSRS design. This suboptimal allocation would cause the TAPAS estimator to perform slightly worse than an SSRS estimator because of the extra random variable introduced, and the SSRS estimator would in turn be no better than an SRS estimator.

The focus of the TAPAS design is to reduce the sampling variance in estimating biomass based upon the degree to which acoustic backscatter corresponds with trawl CPUE. Each of these measures shows a relationship with true fish density, and systematic biases relative to true density may exist in either measure because of processes such as fishes herding to trawl nets or responding to vessel noise. For Alaskan groundfishes, it is commonly assumed that trawl CPUE is less variable than acoustic backscatter as a measure of fish density (over the path of the trawl), although scenarios could occur where this assumption was not realistic (Fréon and Misund, 1999). Information that addresses systematic biases, such as catchability and availability of fish to a sampling method, could be incorporated into the TAPAS design, although this approach would not address the central issue of the imprecision of survey estimates that result from variable spatial distributions of rockfish. For stocks with quantitative stock assessment models, the degree of systematic biases potentially can be addressed by estimating catchability and gear selectivity parameters.

The stratum-wide TAPAS and SRS estimates of biomass were calculated with the following formulae based on Everson et al. (1996):

$$\hat{D}_0=\frac{\sum_{1}^{n-I}\hat{d}_i}{n-I}, \tag{1}$$

$$\hat{D}_1=\frac{\sum_{I}^{I}l_i\hat{d}_i}{l'}, \tag{2}$$

$$\hat{B}_0=A\hat{D}_0\left(1-\frac{l'}{L}\right), \tag{3}$$

$$\hat{B}_1=A\hat{D}_1\frac{l'}{L}, \tag{4}$$

$$\hat{B}=\hat{B}_0+\hat{B}_1, \tag{5}$$

$$\Rightarrow\hat{B}=A\left(\hat{D}_0\left(1-\frac{l'}{L}\right)+\hat{D}_1\frac{l'}{L}\right), \tag{6}$$

$$\hat{B}_{SRS}=A\frac{\sum_{1}^{n-I^*}\hat{d}_i}{n-I^*}, \tag{7}$$

where $\hat{D}_0$ = the mean CPUE (kg/km^2) of the background trawls;
n = the total sample size;
I = the total number of patches encountered;
$\hat{d}_i$ = the CPUE (kg/km^2) of trawl i;
$\hat{D}_1$ = the mean CPUE of the patch trawls;
l' = the total track length within patches;
$\hat{B}_0$ = the estimated biomass for swept areas at background stations (kg);
A = the total sampling area (km^2);
L = the total length (km) of the trackline traveled by the vessel throughout this study;
$\hat{B}_1$ = the estimated biomass for swept areas at patch stations (kg);
$\hat{B}$ = the TAPAS estimate of total biomass in the sampling area;
$\hat{B}_{SRS}$ = the SRS estimate of total biomass in the sampling area; and
I^* = the number of patches that were not planned stations.

The variance derived in Equation 7 of Everson et al. (1996) left out covariance and area terms. We derived an improved estimator of the variance (Table 1) using the delta method (Quinn and Deriso 1999); this derivation is presented in the Appendix. We computed confidence intervals with the "log-Bayes" method suggested by Everson et al. (1996). Finally, we computed SRS and TAPAS confidence intervals with the bootstrap method (Efron and Tibshirani, 1993). In complex sampling designs, there are alternative ways to bootstrap confidence intervals (Rao and Wu, 1988; Smith, 1997; Christman and Pontius, 2000). For our study, we examined several bootstrap methods and found that the results among them were similar. Thus, for comparison with analytical results, bootstrapping was conducted as suggested

Table 1

Biomass and variance estimators for 2 sampling designs, simple random sampling (SRS) and Trawl and Acoustic Presence/Absence Survey (TAPAS), the latter of which was evaluated as a way to reduce the variability in estimated biomass for Pacific ocean perch (*Sebastes alutus*). $\hat{B}$=estimated biomass (kg), $\hat{d}_i$=estimated catch per unit of effort (CPUE, kg/km^2) in trawl i, $\bar{d}$=the mean CPUE, A=total sampling area (km^2), a=the amount of A sampled (km^2), n=total sample size, $\hat{p}$=the estimated proportion of the trackline in patches, l_i=the estimated length (km) of trackline in patch i, l'=the estimate of length (km) of total trackline in patches, $\bar{l}$=the mean patch length, and L=the length of the entire trackline, I=the number of patches, I^*=the number of patches excluding those originally in the background, and $\hat{n}_L$=an estimate of the effective number of independent samples on the trackline; the denominator of 12 was derived from the range parameter of the acoustic variogram.

Estimator	Biomass	Variance
SRS	$\hat{B}_{SRS}=A\frac{\sum_1^{n-I^*}\hat{d}_i}{n-I^*}$	$\hat{V}\left[\hat{B}\right]=\left(1-\frac{a}{A}\right)A^2\left(\begin{array}{l}(1-\hat{p})^2\hat{V}\left[\hat{D}_0\right]+\hat{p}^2\hat{V}\left[\hat{D}_1\right]\\+\left(\hat{D}_0-\hat{D}_1\right)^2\hat{V}[\hat{p}]\\+2\hat{p}\left(\hat{D}_1-\hat{D}_0\right)C\hat{o}v\left[\hat{D}_1,\hat{p}\right]\end{array}\right)$
TAPAS	$\hat{B}=A\left(\begin{array}{l}\frac{\sum_1^{n-I}\hat{d}_i}{n-I}\frac{L-l'}{L}\\+\frac{\sum_{n-I+1}^{n}l_i\hat{d}_i}{l'}\frac{l'}{L}\end{array}\right)$	$\hat{p}=\frac{l'}{L}$
		$\hat{V}\left[\hat{D}_0\right]=\frac{1}{n}\frac{\sum_1^{n-I}(\hat{d}_i-\bar{d})^2}{n-I-1}$
		$\hat{V}\left[\hat{D}_1\right]=\frac{1}{L^2}\left(\frac{\sum_{n-I+1}^{n}\hat{p}_i^2(\hat{d}_i-\bar{d})^2}{(n-I-1)\hat{p}^2}+\bar{d}^2\sum_{n-I+1}^{n}\frac{\hat{p}_i-\frac{\hat{p}_i}{\hat{p}}}{\hat{p}^2\hat{n}_L}\right)$
		$\hat{V}[\hat{p}]=\frac{\hat{p}(1-\hat{p})}{\hat{n}_L}$
		$\hat{n}_L=L/12$
		$C\hat{o}v\left[\hat{D}_1,\hat{p}\right]=\left(\begin{array}{l}\sum_{i=1}^{I}C\hat{o}v\left(\hat{d}_i,\hat{p}_i\right)\frac{\hat{p}_i}{\hat{p}}+\\\sum_{i=1}^{I}\sum_{j=1}^{I}\left(C\hat{o}v\left(\hat{p}_i,\hat{p}_j\right)\frac{\hat{d}_i\hat{p}-\sum_{k=1}^{I}\hat{p}_k\hat{d}_k}{(\hat{p})^2}\right)\end{array}\right)$

by Everson et al. (1996): pairs of patch lengths and associated values of patch CPUE were resampled to preserve any correlation between patch length and CPUE. The number of patches selected was parametrically bootstrapped by drawing from a Poisson distribution with the realized number of patches as the mean of the distribution. An additional Poisson random variable was drawn to determine whether a patch station was included in the SRS estimator. The mean of this second Poisson distribution was the number of planned stations that occurred in a patch during the survey. This source of variability reflects the probability that any of the observed patch stations could have been located at one of our planned stations. Bootstrapping was conducted 10,000 times with the R statistical package (R Development Core Team, 2009). For the TAPAS estimators, both the CPUE values and the patch lengths were resampled with replacement, but, for the SRS estimator, only the CPUE values were resampled. Percentile confidence intervals were constructed with the bias-corrected method of Efron and Tibshirani (1993) that was used in Everson et al. (1996). This method centers intervals on the analytically estimated mean.

To improve the precision of the biomass estimates obtained with our planned design, we re-analyzed the data with alternative patch definitions. First, we examined the relationships of trawl CPUE to other variables, such as the maximum S_v, variance or standard deviation of S_v, median S_v, depth, products and ratios of these quantities, and multiple regressions. These examinations were done to see if focusing on different quantitative characteristics of the acoustic backscatter could result in an improved threshold. We then chose a number of alternative patch definitions and, with the

Table 2

Catch (kg), number of individuals, and mean fork length (cm) of fish and associated coefficient of variation (CV) for the top species caught during our experimental rockfish acoustic–trawl survey conducted in 2009 near Yakutat, Alaska.

Common name	Scientific name	Weight (kg)	Number of individuals	Mean fork length (cm)	Length CV (%)
Pacific ocean perch	*Sebastes alutus*	16,603	27,276	32.3	19
Walleye pollock	*Theragra chalcogramma*	3110	3988	45.8	12
Shortraker rockfish	*Sebastes borealis*	2173	426	65.3	15
Arrowtooth flounder	*Atheresthes stomias*	1738	1506	37.6	32
Shortsp ine thornyhead	*Sebastolobus alascanus*	1020	5131	24.0	27
Dover sole	*Microstomus pacificus*	789	963	40.2	15
Sablefish	*Anoplopoma fimbria*	775	292	61.0	20
Dusky rockfish	*Sebastes variabilis*	426	262	46.1	5
Silvergray rockfish	*Sebastes brevispinis*	381	167	54.8	13
Jellyfish	*Chrysaora melanaster*	320	187	—	—
Other		2836	8444	—	—

best alternative, estimated biomass and precision for comparison with our original field results.

We examined the spatial structure of the S_v along the entire trackline and fish densities from trawls using classical method of moments sample variograms (Cressie, 1993). We also re-examined the densities of POP in trawls from an ACS experiment conducted in 1998 (Hanselman et al., 2001), during which trawls were conducted at a higher spatial resolution (i.e., closer together) than they were in our 2009 study. We coarsened the spatial resolution (upscaled the support) of the acoustic data by aggregating the S_v values so that the distance between S_v values was 1 km, which was the sampling resolution (support) of the trawl data (Atkinson and Tate, 2000). We varied the maximum distance of spatial correlation until a clear range was identified. We then fitted different variogram models (spherical, circular, exponential, and linear) to determine the best shape of the variogram model.

Results

Field sampling occurred during daylight hours over 12 days in August 2009. A total of 59 trawls were completed, with 40 background trawls and 19 patch trawls (Fig. 2). The total weight of all species caught was 30.1 metric tons (t). POP made up 55% of the overall catch from our study, followed by walleye pollock and shortraker rockfish (*S. borealis*) (Table 2). Mean CPUE of POP was 42,450 kg/km^2 in patch trawls and 7,475 kg/km^2 in background trawls. The total trackline covered was 1250 km; 112 km of this total was in patches where we trawled. Overall, about 20% of the trackline (230 km) was above the threshold S_v but was either not long enough to invoke our patch definition or deemed untrawlable by the captain of the FV *Sea Storm*. A return to trawl inside patch stations added an additional travel cost of about 2% beyond the cost of trawling only at planned stations. The last 2 of the 59 trawls were conducted after our planned trackline was completed, and the stations of these 2 trawls were identified with an alternative patch definition (see discussion later in this section); therefore, we did not use them in our main analysis.

Before comparing S_v measurements with trawl densities, we checked for normality of the data. The distribution of S_v along the trackline was reasonably normal (Fig. 4), but trawl densities of POP were left-skewed and required transformation to approach normality. Hanselman and Quinn (2004) showed that power transformations were superior to the logarithm for POP survey data. Applying the Box-Cox power transformation showed that the likelihood surface at different powers was relatively flat between 0.1 and 0.3. We chose to use the fourth-root of trawl CPUE because it showed a better residual pattern and had higher correlation with S_v than did the logarithm and lower power transformations. The relationship between S_v and POP CPUE was relatively weak, particularly below –70 dB (Fig. 5). The relationship between POP CPUE and patch length was tenuous, with a low correlation coefficient (r=0.08). In some cases when our patch algorithm detected a patch, schools of POP appeared to dissipate or move off the seafloor in the time it took to return to the same location and set up a trawl (Fig. 6).

The resulting biomass estimates were very similar among the different types of estimators (Table 3, Fig. 7). All estimates of biomass from our study were much more precise, in terms of the coefficient of variation (CV), than estimates of biomass based on data for the same area from the NMFS GOA trawl survey conducted in 2009 (Fig. 7). The bootstrap procedure yielded similar estimates of biomass and precision between the TAPAS and SRS estimators. If we included the 2 trawls conducted opportunistically off the planned trackline, on the basis of our alternative patch definition, the TAPAS design, with much higher biomass estimates,

performed better than the SRS design (CV=27% vs. CV=34%).

We examined our results with respect to the variables that would have produced a better correlation with trawl CPUE. The weak relationship between S_v and POP CPUE was obtained when comparing only for the length of the trawl trackline (offset for trawl distance behind the vessel). Higher correlations between acoustic backscatter and trawl CPUE resulted when acoustic backscatter was calculated from segments that were centered at the trawl track and 3–5 times the length of the trawl trackline than from segments that were only the length of the trawl trackline. We derived 4 new patch definitions, using a 3-trawl-length sampling window (~3 km), in addition to the patch definitions we used in the field (Table 4). We show results as if we had used the patch definition with the best relationship between S_v and POP density in the field.

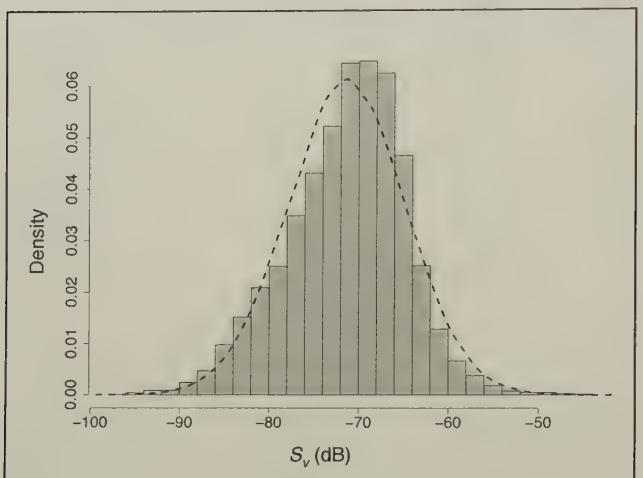

Figure 4

Distribution of values of mean volume backscattering (S_v) for 100-m segments over the trackline (n=12,998 segments) surveyed during our 2009 acoustic–trawl survey. The dashed line is a density plot of a normal distribution with the same mean and standard deviation.

Comparing these patch definitions, we found that the strongest predictor of POP CPUE was the one that used the 90th percentile of maximum S_v in a 3-trawl-length sampling window, which approximated the window we used for our 2009 survey (Fig. 8). This sampling window also gave the lowest error rate in identifying areas of below-average CPUE as a patch station when they should not be (Table 5). The standard deviation of the 3-trawl-length sampling window also performed reasonably well. Alternative 5, one of the alternative patch definitions (Table 4), was attempted to combine backscatter variability and maximum S_v, but it did not perform better than maximum S_v alone. The addition of depth as a variable to any of these alternatives in a multiple regression yielded minor, insignificant improvements to the model.

As a basis for a modified patch definition, we re-analyzed the acoustic data using an S_v criterion of −58.11 dB derived from the 90th percentile of the maximum S_v from the original 2005 FV *Sea Storm* data in our 31-cell window. Only 8 of the previous 19 patch stations were located in patches under this new definition.

Because of this smaller sample size, SRS estimates were less precise with this new patch definition than with the original patch definition. However, despite the smaller sample size, the new threshold for TAPAS did yield a slightly improved CV than the CV obtained with the original threshold (Table 3). Overall biomass estimates were slightly higher, and all measures of precision yielded similar results (Table 3).

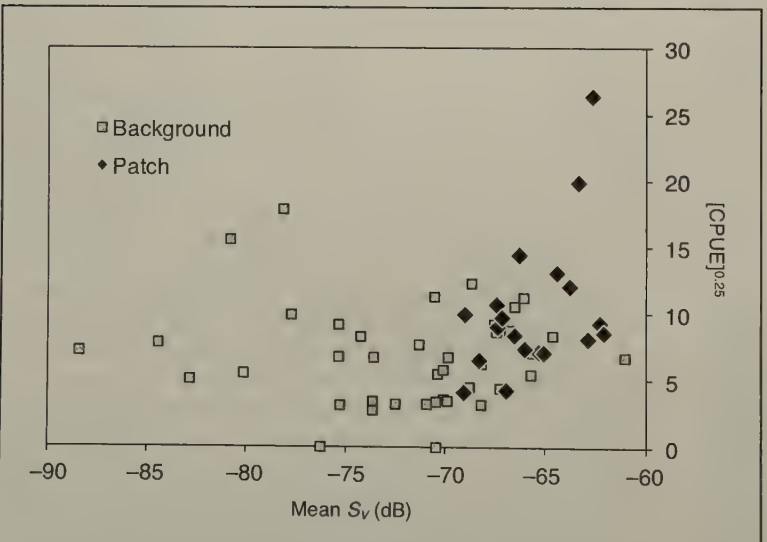

Figure 5

Fourth-root transformed Pacific ocean perch (*Sebastes alutus*) catch per unit of effort (CPUE) versus mean volume backscattering (S_v) per trawl from our 2009 acoustic–trawl survey. Light gray squares indicate background stations, and black diamonds indicate patch stations.

Variogram analysis of the S_v measurements showed strong spatial correlation at the spatial resolution of the trawl data (Fig. 9A). Variogram analysis of the values of trawl CPUE collected during our study revealed no appreciable spatial structure, likely because the trawls were relatively far apart (146 km on average). Alternatively, we compared the S_v measurements from our 2009 study with the values of CPUE collected during an ACS experiment conducted in 1998 (Hanselman et al. 2001); CPUE data were collected at a finer scale (27 km on average) in the ACS experiment than in our study (Fig. 9B). We fitted a spherical model to the S_v measurements and a linear model to the trawl CPUE on the basis of visual fit

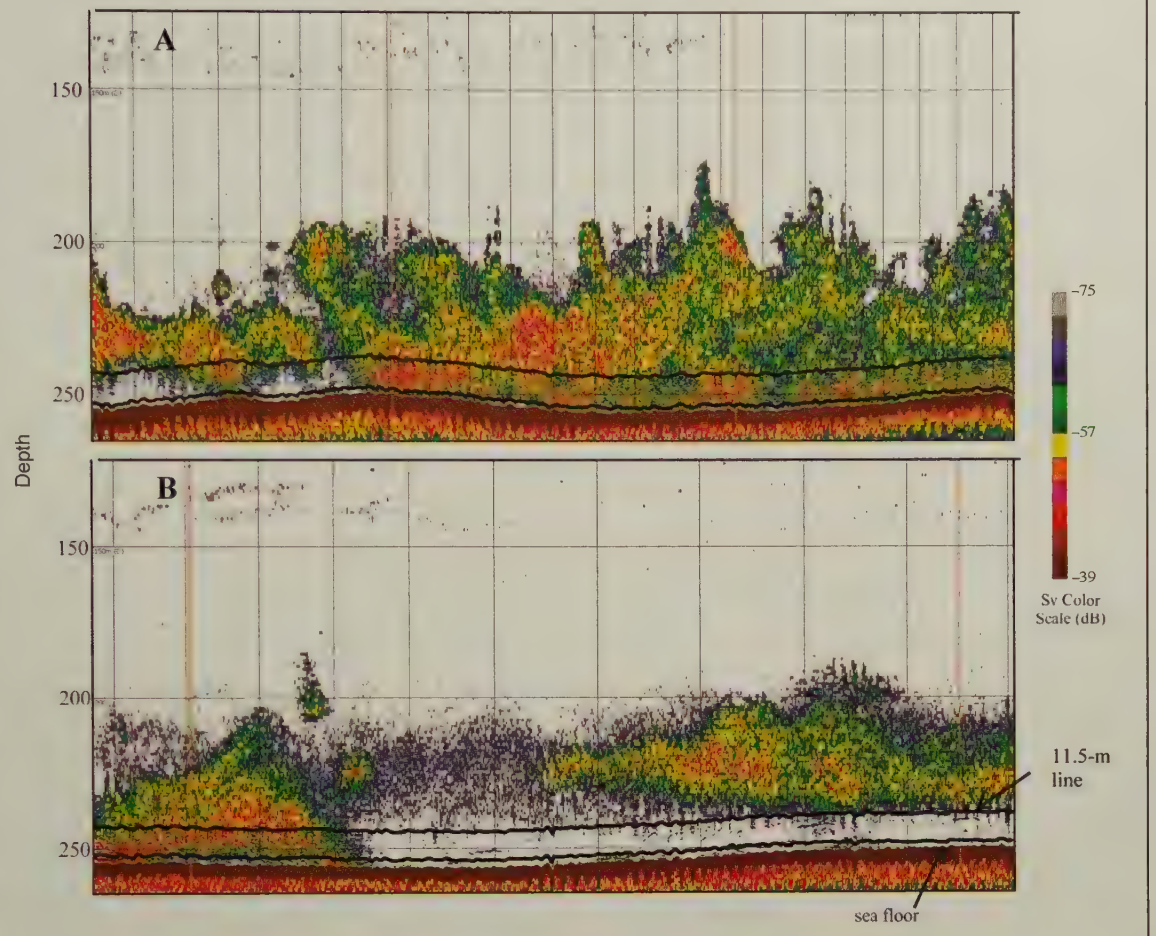

Figure 6

Acoustic backscatter observed (**A**) during patch detection and (**B**) after returning to a trawl location. The black vertical lines mark 100-m distance intervals, the orange vertical lines mark the distance sampled with the trawl, the thick black horizontal lines show the 10-m conformal integration window.

and goodness of fit (coefficient of determination, r^2). The range of correlation for the S_v measurements was larger (~13 km) than the range of correlation for the trawl densities (~8 km). The variogram for the trawl CPUE data had a relatively larger nugget, or unexplained microscale variance, than the variogram for the S_v data.

Discussion

The study area, Yakutat, and target species, POP, for our field study were chosen to increase the likelihood of obtaining a strong relationship between acoustic backscatter and trawl CPUE. Several previous studies had observed relatively strong relationships for rockfishes between S_v and trawl CPUE in the GOA (Krieger et al., 2001; Hanselman and Quinn, 2004; Fujioka et al., 2007), and the Yakutat area was known to have high rockfish abundance. Additionally, Hanselman and Quinn (2004) and Fujioka et al. (2007) showed that stratifying by acoustic backscatter or double sampling could improve precision of biomass estimates on the basis of data collected during previous ACS surveys for rockfishes and biennial NMFS GOA trawl surveys. The use of real-time processing of acoustic backscatter to determine patches was efficient, and POP were the most commonly caught species and were found in higher densities than other fishes at patch stations. However, the conditions that make the TAPAS design more efficient than random sampling, as shown in simulation studies (Spencer et al., 2012), did not materialize in the fieldwork described here.

For the TAPAS design to be more effective than SRS, the categorization of patch and background areas must show a correspondence with trawl CPUE (i.e., CPUE values consistently should be higher at the patch stations than at the background stations). When this correspondence does not occur, the use of these categories does not improve the precision of biomass estimates and increases variability because the sizes of the patch

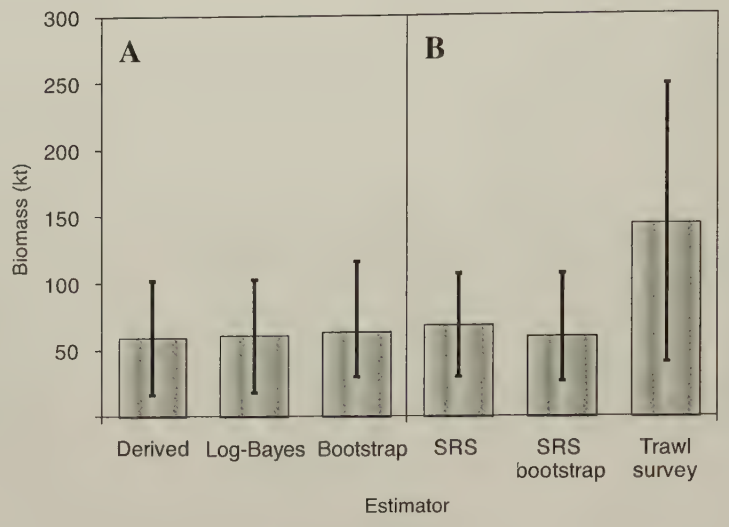

Figure 7

Comparison of bootstrap versus derived analytical results for the estimators for the Trawl and Acoustic Presence/Absence Survey (TAPAS) sampling design, with (**A**) a proportion of the 80th percentile of the mean volume backscattering (S_v) in a 31-cell window and (**B**) simple random sampling (SRS) and the 2009 NMFS trawl survey in the same area. Analytical confidence intervals are approximately 95% (±2 standard deviation). Bootstrap confidence intervals are bias-corrected 95% percentile intervals.

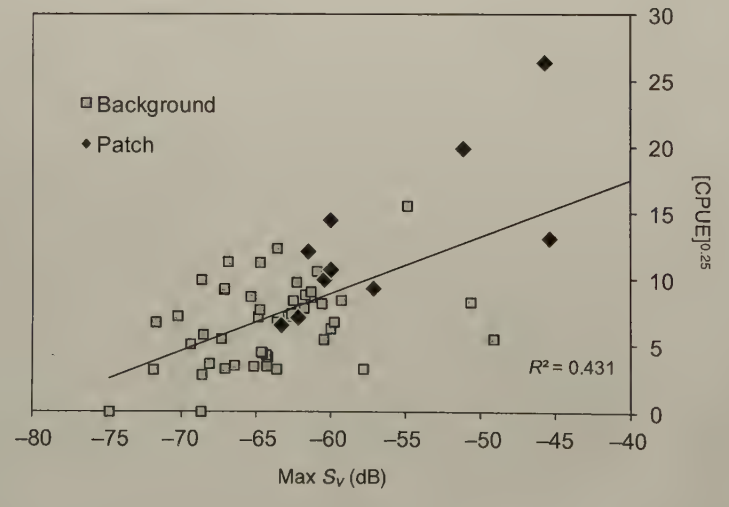

Figure 8

Relationship of maximum mean volume backscattering (S_v) to the fourth root of Pacific ocean perch (*Sebastes alutus*) catch per unit of effort (CPUE), from our 2009 acoustic–trawl survey, in an acoustic sampling window with a length of 3 trawls (~ 3.0 km). Light gray squares indicate background stations, and black diamonds indicate patch stations.

and background areas are estimated. Despite the minimal requirement of classifying the acoustic data into only 2 categories, the results of our study indicate that the effectiveness of the TAPAS design remains dependent upon the strength of the relationship between S_v and trawl CPUE. Patch size and CPUE were only weakly correlated, and the variance of the planned stations was not as high as expected. Variogram analysis of ACS data showed that the spatial correlation range for trawl CPUE may be smaller than the range for S_v data. Previous variograms estimated for the NMFS GOA trawl surveys had indicated a range of ~4.5 km (Hanselman et al. 2001), which was also smaller than the range of the acoustic backscatter collected in our study. The larger range of the S_v data may indicate that some of the intensity of S_v is a result of ambient variables other than POP density. The nugget (unexplained variance) of the trawl CPUE is large, relative to the total variance for the trawl CPUE, an indication that the trawl CPUE data likely have more measurement error than the acoustic data and that the data were sparser. The trawl CPUE variogram in our study had a larger range than did the individual areas analyzed in Hanselman et al. (2001). This difference in range could have occurred because the aggregated data in our study had more pairs of trawl densities at larger lag distances than did the spatially explicit variograms with smaller sample sizes in that earlier study.

One source of discrepancy between the acoustic and trawl data is that multiple species contribute to the acoustic backscatter. Von Szalay et al. (2007) had success relating acoustic backscatter of walleye pollock with CPUE in the Bering Sea. However, walleye pollock make up the majority of the biomass in the Bering Sea; in contrast, POP is one of a number of abundant species in the GOA. Krieger et al. (2001) had more success relating acoustic backscatter with rockfishes using a Simrad EK500 quantitative echosounder. In their study, which was conducted in the more rugged habitat off Southeast Alaska, the catch was primarily rockfishes and contained species that were smaller in size than the larger rockfish species and walleye pollock that made up the non-POP catch in our study. Although we restricted our study area to depths where POP would be the dominant species and, indeed, where POP was the largest component of our catch, our origi-

nal sampling algorithm revealed patches of acoustic backscatter that were not characteristic of rockfishes. Steadier and less intense than backscatter associated with rockfishes, these patches may have been caused by squid (*Berryteuthis* spp.) or eulachon (*Thaleichthys pacificus*). In addition, a substantial amount of walleye pollock was caught coincident with POP catches. The TAPAS design may perform better in multispecies situations because of the relatively relaxed requirement of categorizing data into 2 groups, as opposed to the more involved effort of a statistical regression required for double sampling in a regression design.

Differences in the portions of the water column surveyed by the 2 sampling methods also can lead to low correspondence between acoustic and trawl data. Rockfishes can be closely associated with the seafloor and, perhaps, in the acoustic dead zone, but walleye pollock and other species are typically observed higher in the water column. We also noted the ephemeral nature of fish schools (Fig. 6), which may be attributed to responses to vessel noise or to changes in the position of fishes in the water column for foraging. Diurnal and seasonal changes in the level of aggregation clearly could hinder the effectiveness of our acoustic algorithm in relation to fish CPUE. Changes of the vertical orientation of POP to the seafloor also could influence backscatter and may have affected our acoustic algorithm (Fréon and Misund 1999).

When the field data from our study were re-analyzed with different patch definitions, we found that CPUE was more strongly related to acoustic backscatter in a window longer than the typical trawl distance—likely a result of the extremely fine spatial structure of schools or to the behavioral reactions of fishes to the initial pass of the FV *Sea Storm* over the patch (Mitson and Knudsen, 2003). If the spatial structure of schools was relatively narrow, then the trawl net may not have passed through the same school that was identified by the echosounder because of currents and imperfect tracking of the original vessel path (Ona and Godø, 1990; Engas et al., 2000). Re-analysis revealed that the use of the 90th percentile of maximum S_v was more successful in identifying stations where rockfish CPUE was high and resulted in slightly more precise biomass estimates, compared with results from the original patch definition, despite a lower sample size. As with the analysis of Hanselman and Quinn (2004) with their ACS simulations, our re-analysis of the acoustic data showed that the TAPAS estimator can be improved when a high criterion of acoustic backscatter is used for the patch definition (i.e., additional sampling is invoked only in a few, high fish-density instances) and essentially outliers are removed from the random sampling portion of the ACS and TAPAS estimators.

The TAPAS design incorporates aspects of both adaptive sampling, which usually consists of a single sampling gear applied to a highly variable spatial distribution, and double sampling designs that rely on sampling primary and auxiliary variables (Thompson, 2002). The TAPAS design provides one operational method for implementing a double sampling for stratification design. The use of acoustics to stratify a survey area was generally recommended by Fujioka et al. (2007) and Hjellvik et al. (2007), with the difference that acoustic backscatter is continuously monitored rather than sampled in discrete units.

Results from our study and the ACS design attempted by Hanselman et al. (2003) highlight that even when focusing specifically on the abundance of rockfishes, it is difficult to survey stocks with high spatial variability that exist on both trawlable and untrawlable grounds. In the ACS surveys of Hanselman et al. (2003) specialized tire gear was used, which made trawling on each cluster station possible, but made comparisons of CPUE impractical between those ACS surveys and surveys that used typical NMFS trawl gear. In our study, we used standard NMFS trawl gear; however, it could not be used in all observed patch stations. If POP were more abundant in some of these untrawlable patches and we had used different gear that would have allowed us to survey those patches, we may have had higher

Table 3

Parameter estimates from 2 sampling designs, Trawl and Acoustic Presence/Absence Survey (TAPAS), and simple random sampling (SRS), with the use of 2 different patch definitions. Patch definitions are based on percentiles of mean or maximum volume backscattering (S_v) from acoustic data collected during our 2009 acoustic–trawl survey. Rockfish densities and biomass estimates are given in metric tons per square kilometers (t/km^2) and metric tons (t), respectively. n=total sample size, I=the number of patches, l'= the estimate of length (km) of total trackline in patches, L=the length of the entire trackline, D_0=the mean background CPUE, D_1=the mean patch CPUE, B_0=the background biomass, B_I=the patch biomass, B=the TAPAS estimate of total biomass (kg), B_{SRS}= the SRS estimate of total biomass. SRS coefficients of variation (CVs) were calculated by using the full sample size (n).

Parameter	80th percentile of mean S_v	90th percentile of max S_v
N–I	40	41
n	57	49
I	17	8
l'	93.6	43.5
L	1251	1251
D_0	7.48	7.43
D_1	9.74	24.82
B_0	53,928	55,898
B_1	5684	6734
B	59,612	62,632
CV_B (analytical)	34.6	34.0
CV_B (bootstrap)	34.5	33.6
B_{SRS}	68,517	68,517
CV_{SRS} (analytical)	27.8	30.0
CV_{SRS} (bootstrap)	30.2	31.9

Table 4

The original method used in our 2009 acoustic–trawl survey and proposed alternative methods for selection of "patches," or areas where catch per unit of effort may have been high, compared with other survey areas, on the basis of acoustic backscatter over a sampling window of 3 trawl lengths. Patch definitions were based on a threshold of mean volume backscattering (S_v). Alternatives were created to maximize the strength of the relationship of S_v to CPUE and improve survey precision.

Original patch definition
The S_v was computed for each 100-m cell within a moving window of 31 cells or 3.1 km. A patch was defined when the proportion of these cells exceeding an S_v value of −65.6 dB was greater than 0.39 (the 80th percentile of the backscatter data collected in the Yakutat, Alaska, area in 2005 aboard the FV *Sea Storm*).
Alternative 1
Higher field threshold definition To account for the uniform and weak nonrockfish backscatter encountered in the field, the S_v threshold was increased to −61.4 dB from the value used in the original method. The threshold for the moving proportion was lowered to 0.13. These values were computed from the 90th and 50th percentiles of our field data, respectively. The rationale for this definition was to detect patches when the acoustic backscatter was more variable but stronger than the backscatter detected as patches with the original patch definition.
Alternative 2
Standard deviation of S_v To capture the tight intermittent clustering of rockfish schools, we used the following threshold: the standard deviation of S_v was above the 80th percentile. The rationale of this definition was to capture some distributional properties associated with rockfish acoustic backscatter.
Alternative 3
Variance to mean ratio of S_v To remove uniform, diffuse acoustic backscatter and account for tight intermittent clustering of rockfish schools, we used the following threshold: the variance-to-mean ratio was above the 80th percentile. The rationale of this definition was to identify a patch when the variance-to-mean ratio moved far above 1 (e.g., departing from a Poisson distribution toward a hypergeometric distribution).
Alternative 4
Maximum S_v If the survey was conducted in a depth stratum and area where the target species was abundant, it was assumed that pulses in maximum S_v should reflect the dominant species. For this alternative, the 90th percentile of maximum S_v was used.
Alternative 5
Maximum S_v and standard deviation of S_v This method refined Alternative 4 by adding variability into the criterion in a multiple regression. The rationale of this definition was similar to the rationale of Alternative 2.

POP densities in our patch trawls. When comparing our estimates with assessments of Hanselman et al. (2003), we found that the CV on mean CPUE was lower at the planned stations in our study than in the SRS portion of the ACS study. Unlike the bimodal bootstrap distribution of the SRS estimates in Hanselman et al. (2003), a relatively Gaussian distribution resulted when bootstrapping the TAPAS and SRS estimators. Both designs have the disadvantage of having a variable sample size, but both have the advantage of completing a survey in a single pass through a study area. The TAPAS design imposed a small additional cost for travel time because our vessel had to return to trawl a random location in a patch, but the daily number of trawls conducted was not affected. The ACS and TAPAS designs are both more efficient than some of other two-stage designs that require the completion of an initial random sample before the second stage can begin. Another challenge with field studies of spatially variable species is that performance of survey designs depends highly on the fish densities encountered in a given survey.

Previous attempts to improve the correspondence between acoustic backscatter and trawl CPUE have focused on partitioning the acoustic backscatter to species (Mackinson et al., 2005) and quantifying relative catchability of these 2 sampling methods (McQuinn et

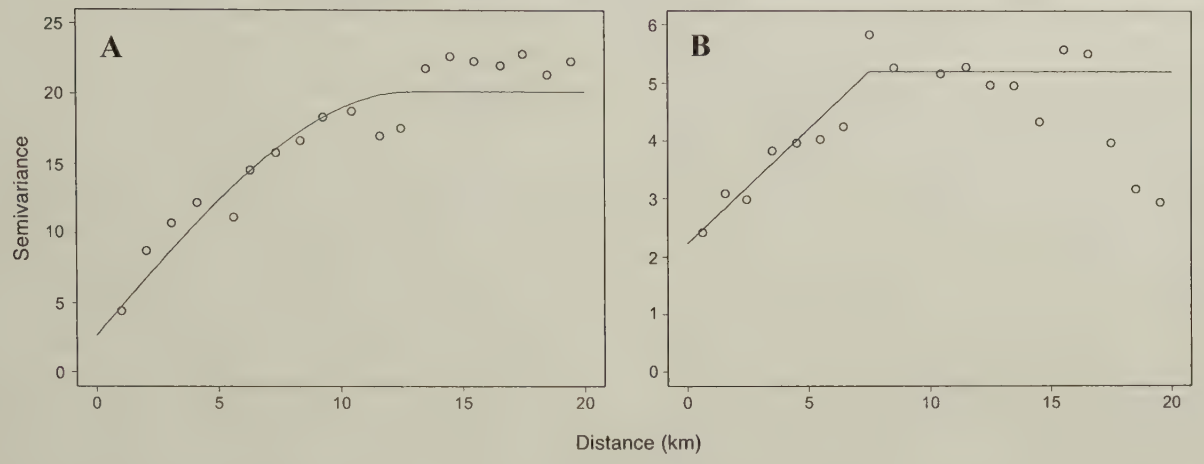

Figure 9

(**A**) Variogram of mean volume backscattering (S_v) from the vessel path (n=669 mean values) sampled during our 2009 acoustic–trawl survey. Line is spherical model fit: range (where spatial correlation ends)=12.9 km, partial sill (explained variance)=17.5 km, nugget (unexplained microscale variance)=2.6 (**B**) Variogram of [CPUE]$^{0.25}$ during the 1998 adaptive-cluster-sampling experiment (n=147 trawls). The line is the linear model fit: range=7.5 km, partial sill=3.0 km, nugget=2.2.

Table 5

Comparison of 5 alternative methods of patch selection to the original design for a 3-trawl-length (~3.0 km) acoustic sampling window.

Patch definition	Description	Selects above average CPUE	Selects below average CPUE	Error rate (%)
Original	80th percentile, 0.38 of the time	14	4	22
1	90th percentile, 0.12 of the time	7	2	22
2	80th percentile of the standard deviation of S_v	4	1	20
3	80th percentile of variance to mean ratio	4	1	20
4	90th percentile of max S_v	6	1	14
5	80th percentile of 1/max S_v×SD (S_v)	4	1	20

al., 2005). Beare et al.[3] found that using the length and species composition information from trawls to partition acoustic backscatter to species improved correlations. Mackinson et al. (2005) used a fuzzy logic approach to examine the relationship between acoustic backscatter and trawl CPUE, and they found that depth was a better predictor of trawl CPUE than was acoustic backscatter. For Alaskan groundfishes, species composition can be inferred relatively accurately by depth (Hanselman and Quinn 2004). Further work should focus on identifying specific characteristics of acoustic backscatter, such as school shape, target strength, and school density that would contrast rockfishes from co-occurring species. However, multivariate analyses have shown that distinguishing POP backscatter from walleye pollock backscatter is challenging (Spencer et al.[4]).

Increased precision for future applications of the TAPAS design could be attained in several ways. Improved correspondence between acoustic backscatter and trawl CPUE, for example, could be obtained from better partitioning of acoustic backscatter to species and quantifying the availability and vulnerability of a fish to these 2 sampling methods. Spencer et al. (2012) showed

[3] Beare, D. J., D. G. Reid, T. Greig, N. Bez, V. Hjellvik, O. R. Godø, M. Bouleau, J. van der Kooij, S. Neville, and S. Mackinson. 2004. Positive relationships between bottom trawl and acoustic data. ICES CM (council meeting) document 2004/R:24, 15 p.

[4] Spencer, P. D., D. H. Hanselman, and D. R. McKelvey. 2011. Evaluation of echosign data in improving trawl survey biomass estimates for patchily-distributed rockfish. North Pacific Research Board Final Report 809, 110 p. [Available from http://doc.nprb.org/web/08_prjs/809_final%20report_revised%20_2_.pdf, accessed September 2011.]

that the highest gains in efficiency for the TAPAS design, compared with SRS in simulations, were achieved when the spatial correlation of fish density was low and there was a large number of patches of small size. Such circumstances resulted in the TAPAS design sampling a high proportion of the total area of patches in the population. In addition, Spencer et al. (2012) showed that a modified TAPAS design, in which every third patch was sampled, resulted in higher efficiency than did an SRS design. However, the situations in Spencer et al. (2012) where there were significant gains in performance relative to SRS occurred only when there was a strong relationship between S_v and CPUE. Everson et al. (1996) showed that precision could be most improved when patches were smallest and they were a low proportion of the total survey area such that the probability of sampling high-CPUE areas during a random survey was low. These results indicate that the TAPAS design may show greater gains in precision for biomass estimates of a stock that is even more concentrated into small areas than is POP.

For these rockfish stocks, the greatest improvement in precision of trawl-survey indices of biomass can be achieved by increasing the overall sample size in the narrow depth band where they are most abundant. The ACS and TAPAS designs are useful frameworks for efficiently adding samples in abundant areas, and they also can serve to improve the NMFS trawl index in specific high-variability strata. Clearly, these designs should be applied only in depths and areas of known high abundance and variability of a species of interest, and the design should use a high threshold for invoking additional sampling.

For the TAPAS design to be applied efficiently, the specific acoustic backscatter characteristics of a target species need to be well known so that the relationships between patch definition, patch length, and CPUE are strong. Under these conditions (e.g., a patch station reliably has high CPUE), it might be beneficial to obtain an additional commercial vessel to follow the primary survey vessel, sample patch stations, and retain the catch, while the primary survey vessel continues to sample planned stations. These cost-recovery surveys (e.g., Hanselman et al. 2003) have been useful in Alaska as zero- or low-cost alternatives to the normal practice of discarding catch on purely random surveys.

Even if a design that combines acoustic surveys and trawl surveys could provide superior estimates of biomass, in practice, such a design would have to be modified to a context of a multispecies groundfish survey in most situations. Such adaptation is an additional complication in the use of novel sampling designs, given the competing sampling goals and limited resources of fisheries monitoring. In a multispecies context, the TAPAS design may be a way to add more sampling effort for major species groups that occupy a similar depth or area when differentiation of backscatter is difficult (as it is for rockfishes and walleye pollock). An avenue of future research would be to examine the precision of biomass estimates determined with the TAPAS design for multiple species that produce significant acoustic backscatter.

Conclusions

Our work shows that sampling fish populations with high spatial variability remains a challenge. To more accurately understand acoustic and spatial patterns for POP and other rockfishes, it may be necessary to consider more quantitative acoustic or geostatistical methods and to move away from the traditional paradigm of bottom trawl surveys (Godø, 2009). However, in areas that are fortunate enough to have a long time series of standardized fishery-independent surveys, it is rare and, perhaps, unwise to make changes to the sampling design or the sampling method. TAPAS and analogous designs could be used to increase sampling intensity for specific stocks, without necessarily creating a break in a biomass time series. The potential improvement in the precision of biomass estimates through the use of the TAPAS design when a strong relationship exists between S_v and CPUE (Spencer et al., 2012) offers motivation for continuing to refine our understanding of acoustic and spatial patterns and the methods used to define high-CPUE patches.

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Appendix

This appendix outlines the method with which we derived TAPAS variance estimators. Capital letters denote random variables; lower case letters denote realized values of random variables. This formulation redefines l'/L as an estimate of p, which is the proportion of the survey area in the patches, so that the properties of the binomial distribution can be used to capture the variability of track lengths of patches. Overbar notation refers to the mean, and hat notation refers to a sample estimate.

Definitions

p–Proportion of survey area in patches,

$$\frac{l'}{t},$$

a–Total area swept by bottom trawl, A–Total area of sampling area, D_0–Mean background CPUE, B_0–Background biomass, $AD_0(1-p)$, t–Total track length, l'–Total track length within patches,

$$l'=\sum_{I} l_i,$$

l_i–Length of track in patch i, I–Total number of patches encountered, L–Sum of length in patches, L_i–Length of patch i, $\bar{D}_i$–Mean CPUE within patch i, D_1–Mean patch CPUE in all patches,

$$D_1=\frac{\sum_{I} L_i \bar{D}_i}{L},$$

B_1–Patch biomass,

$$A\frac{\sum_{I} L_i \bar{D}_i}{t}=AD_1 p,$$

B– B_0 + B_1, B–Total biomass

$$\Rightarrow B=AD_0(1-p)+AD_1 p=A\left(D_0(1-p)+D_1 p\right).$$

Biomass variance

After defining the variables, we derived the variance of the overall biomass estimate ($V[B]$):

$$V[B]=A^2 V\left[D_0(1-p)+D_1 p\right].$$

We used the definition of the variance of a sum:

$$V[B]=A^2\left(V\left[D_0(1-p)\right]+V\left[D_1 p\right]+2Cov\left[D_0(1-p),D_1 p\right]\right).$$

We applied the definition of the variance of a sum again:

$$V[B]=A^2\left(V\left[D_0-D_0 p\right]+V\left[D_1 p\right]+2Cov\left[D_0(1-p),D_1 p\right]\right),$$

$$V[B]=A^2\begin{pmatrix}V\left[D_0\right]+V\left[D_0 p\right]+2Cov\left[D_0,-D_0 p\right]+V\left[D_1 p\right]\\ +2Cov\left[D_0(1-p),D_1 p\right]\end{pmatrix}.$$

We removed constants and re-arranged the equation so that covariance terms were at the end:

$$V[B]=A^2\begin{pmatrix}V\left[D_0\right]+V\left[D_0 p\right]+V\left[D_1 p\right]-2Cov\left[D_0,D_0 p\right]\\ +2Cov\left[D_0(1-p),D_1 p\right]\end{pmatrix}.$$

We defined parts to simplify the derivation with the delta method:

$$P=V\left[D_0 p\right],$$
$$Q=V\left[D_1 p\right],$$
$$R=Cov\left[D_0,D_0 p\right],$$
$$S=Cov\left[D_0(1-p),D_1 p\right],$$
$$V[B]=A^2\left(V\left[D_0\right]+P+Q-2R+2S\right).$$

Part P:

$$P=E\left[\frac{\partial D_0 p}{\partial D_0}\right]^2 V[D_0]+E\left[\frac{\partial D_0 p}{\partial p}\right]^2 V[p]+ 2E\left[\frac{\partial D_0 p}{\partial D_0}\right]E\left[\frac{\partial D_0 p}{\partial p}\right]Cov[D_0,p]$$

$$P=E[\hat{p}]^2 V[D_0]+E[D_0]^2 V[\hat{p}] +2E[D_0]E[\hat{p}]Cov[D_0,\hat{p}].$$

Part Q:

$$Q=E\left[\frac{\partial D_1 p}{\partial D_1}\right]^2 V[D_1]+E\left[\frac{\partial D_1 p}{\partial p}\right]^2 V[p] +2E\left[\frac{\partial D_1 p}{\partial D_1}\right]E\left[\frac{\partial D_1 p}{\partial p}\right]Cov[D_1,p]$$

$$Q=E[p]^2 V[D_1]+E[D_1]^2 V[p] +2E[D_1]E[p]Cov[D_1,p].$$

Part R:

$$R=E\left[\frac{\partial D_0}{\partial D_0}\right]E\left[\frac{\partial (D_0 p)}{\partial D_0}\right]V[D_0] +E\left[\frac{\partial D_0}{\partial \hat{p}}\right]E\left[\frac{\partial (D_0 p)}{\partial p}\right]V[p]$$

$$+E\left[\frac{\partial D_0}{\partial D_0}\right]E\left[\frac{\partial (D_0 p)}{\partial p}\right]Cov[D_0,p] +E\left[\frac{\partial D_0}{\partial p}\right]E\left[\frac{\partial (D_0 p)}{\partial D_0}\right]Cov[p,D_0]$$

$$R=E[p]V[D_0]+E[D_0]Cov[D_0,p].$$

We aggregated the parts:

$$V[B]=A^2\left(V[D_0]+P+Q-2R+2S\right),$$

$$V[B]=A^2\begin{pmatrix} V[D_0]+E[p]^2 V[D_0]+E[D_0]^2 V[p] \\ +2E[D_0]E[p]Cov[D_0,p]+ \\ E[p]^2 V[D_1]+E[D_1]^2 V[p] \\ +2E[D_1]E[p]Cov[D_1,p]+ \\ -2\left(E[p]V[D_0]+E[D_0]Cov[D_0,p]\right)+ \\ +2\begin{pmatrix} E[1-p]E[D_1]Cov[D_0,p] \\ -E[D_0]E[D_1]V[p] \\ -E[D_0]E[p]Cov[D_1,p] \end{pmatrix} \end{pmatrix}.$$

We rearranged the terms (covariance between D_0 and $\hat{p}$ was assumed to be zero):

$$V[B]=A^2\begin{pmatrix} \left(1-E[p]\right)^2 V[D_0]+E[p]^2 V[D_1]+ \\ \left(E[D_0]-E[D_1]\right)^2 V[p] \\ +2E[p]\left(E[D_1]-E[D_0]\right)Cov[D_1,p] \end{pmatrix}.$$

We estimated the biomass variance by replacing expected values with sample statistics:

$$\hat{V}[\hat{B}]=\left(1-\frac{a}{A}\right)A^2\begin{pmatrix} (1-\hat{p})^2\hat{V}[\hat{D}_0]+\hat{p}^2\hat{V}[\hat{D}_1] \\ +\left(\hat{D}_0-\hat{D}_1\right)^2\hat{V}[\hat{p}] \\ +2\hat{p}\left(\hat{D}_1-\hat{D}_0\right)C\hat{o}v[\hat{D}_1,\hat{p}] \end{pmatrix},$$

whereas $\left(1-\frac{a}{A}\right)$ was the finite population correction.

Derivation of the variance of the estimates of p, D_0, and D_1

Variance of the estimate of p:

Each patch accounted for some proportion of the total length of the trackline so that $p_i=L_i/t$. We were interested in the overall proportion of the trackline that was in the patches, or p. The parameter p was considered to be a parameter of a binomial distribution. In a binomial distribution, an estimate of p is X/n, where X was the number of successes in n discrete observations. In our TAPAS application, the total of the discrete observations was $\hat{n}_L$ (the number of 100-m segments along the survey trackline) and X was the number of these observations that were in a patch. Our sample estimate of X/n was $\hat{p}$ with the binomial estimated variance:

$$\hat{V}[\hat{p}]=\frac{\hat{p}(1-\hat{p})}{\hat{n}_L}.$$

These $\hat{n}_L$ observations could have been assumed to be independent, but there was likely some spatial correlation. For our application, variogram analysis of acoustic backscatter data indicated that the range parameter was ~12 km. This range resulted in an effective sample size that was much smaller than the total number of discrete sampling units, and variance was underestimated. The value of $\hat{n}_L$ used in the variance equation should reflect this autocorrelation. In our application, we divided our total trackline length (~1200 km) by the variogram range parameter (~12 km), a calculation that yielded an $\hat{n}_L$ ~100.

Variance of the estimate of D_0:

The variance in D_0 was the straightforward random sampling estimator shown as the variance of $\hat{D}_0$ in Table 1.

Variance of the estimate of D_1:

Recall that D_1 was estimated as

$$D_1=\frac{\sum_{i=1}^{I}L_i\overline{D}_i}{L}.$$

We expressed the L_i in terms of p and made substitutions to obtain

$$D_1=\frac{\sum_{i=1}^{I}p_i\overline{D}_i}{\sum_{i=1}^{I}p_i}=\frac{\sum_{i=1}^{I}p_i\overline{D}_i}{p}=\sum_{i=1}^{I}z_i\overline{D}_i,$$

where $z_i = p_i/p$.

This expression rescaled the values of p_i so that they summed to one. In this case, we observed a given number of "samples" of trackline from the patches, and z_i was the proportion of all the patch trackline that was in patch i. This calculation was still a binomial distribution, except, in this case, we ignored the background category and were concerned only with the patches.

We applied the delta method to this sum of products of random variables:

$$V\left[\sum_{i=1}^{I}z_i\overline{D}_i\right]=\sum_i\left(V[z_i]E\left[\overline{D}_i\right]^2+V\left[\overline{D}_i\right]E[z_i]^2\right)+2\sum_{i\neq j}E\left[\overline{D}_i\right]E[z_j]Cov(\overline{D}_i,z_j).$$

The variance of z_i could be obtained with the same method as that for the variance of p, with an adjusted n_L. We substituted sample statistics for expected values to obtain the estimated variance of D_1:

$$\hat{V}\left[\hat{D}_1\right]=\frac{1}{L^2}\left(\frac{\sum_{n-I+1}^{n}\hat{p}_i^2(\hat{d}_i-\overline{d})^2}{(n-I-1)\hat{p}^2}+\overline{d}^2\sum_{n-I+1}^{n}\frac{\hat{p}_i-\hat{\hat{p}}}{\hat{p}^2\hat{n}_L}\right).$$

In theory, the term for Cov($\overline{D}_i$, z_j) should be a nonzero value. For example, consider a case with 2 patches. If the proportion in one patch is large, the proportion in the other patch is small, and CPUE and patch length (the proportion) are correlated, then the CPUE would be small in the patch with the small proportion. However, as the number of patches becomes much greater than 2, the covariance between patches and density decreases as $z_j \rightarrow 0$. We assumed this covariance was negligible:

$$V\left[\sum_{i=1}^{I}z_i\overline{D}_i\right]=\sum_i\left(V[z_i]E\left[\overline{D}_i\right]^2+V\left[\overline{D}_i\right]E[z_i]^2\right).$$

Covariance of $[D_1, p]$:

Recall

$$D_1=\frac{\sum_{i=1}^{I}p_i\overline{D}_i}{\sum_{i=1}^{I}p_i}=\frac{\sum_{i=1}^{I}p_i\overline{D}_i}{p},$$

$$p=\sum_{i=1}^{I}p_i.$$

Here, we did not substitute z_i for p_i/p because the set of p_i was common to both functions. Recall that the covariance of 2 functions of random variables was

$$Cov(g(x),h(x))\cong 2\sum_{i>j}Cov(x_i,x_j)\frac{\partial g}{\partial x_i}\frac{\partial h}{\partial x_j}.$$

In our application, $g(x) = D_1$ and $h(x) = p$.

We applied the delta method:

$$Cov(D_1,\hat{p})=\sum_{i=1}^{I}\sum_{j=1}^{I}\left(Cov\left(\overline{D}_i,p_i\right)\frac{p_i}{p}+Cov\left(p_i,p_j\right)\frac{\overline{D}_i p-\sum_{k=1}^{I}p_k\overline{D}_k}{(p)^2}\right).$$

We used the argument above that Cov ($\overline{D}_i$, p_j) , where $i \neq j$, can be ignored. This argument leaves only the Cov ($\overline{D}_i$, p_i), which, in the sampling design of the TAPAS, was expected to be a nonzero value (i.e., the length of a given patch is correlated with the CPUE of that patch):

$$Cov(D_1,p)=\sum_{i=1}^{I}Cov\left(\overline{D}_i,p_i\right)\frac{p_i}{p}+\sum_{i=1}^{I}\sum_{j=1}^{I}\left(Cov\left(p_i,p_j\right)\frac{\overline{D}_i p-\sum_{k=1}^{I}p_k\overline{D}_k}{(p)^2}\right).$$

We substituted sample statistics to obtain the covariance of $[D_1, p]$:

$$C\hat{o}v\left[\hat{D}_1,\hat{p}\right]=\left(\sum_{i=1}^{I}C\hat{o}v\left(\hat{d}_i,\hat{p}_i\right)\frac{\hat{p}_i}{\hat{p}}+\sum_{i=1}^{I}\sum_{j=1}^{I}\left(C\hat{o}v\left(\hat{p}_i,\hat{p}_j\right)\frac{\hat{d}_i\hat{p}-\sum_{k=1}^{I}\hat{p}_k\hat{d}_k}{(\hat{p})^2}\right)\right).$$

Inshore spawning of cobia (*Rachycentron canadum*) in South Carolina

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Abstract—We documented inshore spawning of the recreationally important cobia (*Rachycentron canadum*) in Port Royal Sound (PRS) and St. Helena Sound (SHS), South Carolina, during the period from April to June in both 2007 and 2008. Histological analysis of ovaries confirmed the presence of actively spawning females inshore, and gonadosomatic index (GSI) values from females collected inshore (mean=7.8) were higher than the values from females caught offshore (mean=5.6); both of these mean values indicate that spawning occurred locally. Additionally, we conducted an ichthyoplankton survey in 2008 and found cobia eggs and larvae as far as 10 and 15 km inshore from the mouths of SHS and PRS, respectively. A study of egg development that we conducted in 2007 and 2008 using hatchery-reared cobia eggs provided descriptions of embryological development of cobia. Comparison of visual and quantitative characteristics of the field-collected eggs with those of the hatchery-reared eggs allowed positive identification of eggs collected in plankton samples. The ages of field-collected eggs and presence of females with hydrated oocytes in PRS and SHS observed in our ichthyoplankton survey and histological analysis indicated that wild cobia spawn in the afternoon and early evening. The inshore migration of cobia from April to June, the presence of actively spawning females, significantly higher GSI values, and the collection of eggs inside PRS and SHS all confirm that these estuaries provide spawning habitat for cobia. Because of the potential for heavy exploitation by recreational anglers as cobia move inshore to spawn in South Carolina, current management strategies may require review.

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Cobia (*Rachycentron canadum*) is a migratory, euryhaline benthopelagic species distributed worldwide in tropic, subtropic, and warm temperate waters, except in the eastern Pacific (Briggs, 1960). In the United States, cobia are found throughout the Gulf of Mexico and along the Atlantic coast from Florida to Massachusetts (Shaffer and Nakamura, 1989). Cobia are moderately long lived, with a maximum reported age of 15 years (Shaffer and Nakamura, 1989), and have fast growth rates, with both sexes reaching sexual maturity by age 2 (males 60 cm fork length [FL]; females 80 cm FL [Smith, 1996; Burns et al.[1]]). Currently in the United States, most commercial landings of cobia result from incidental catch in other fisheries (Shaffer and Nakamura, 1989). Cobia are sought recreationally throughout their range, and the majority of the annual catch for cobia in the United States comes from the recreational fishery: 957 of the combined 1070 metric tons (t) from commercial and recreational landings in 2010 (National Marine Fisheries Service [NMFS[2]]). The current fishery management plan for cobia, which imposes a bag limit of 2 fish per person per day and a minimum FL of 84 cm (33 in), was established by the Gulf of Mexico Fishery Management Council (GMFMC) and South Atlantic Fishery Management Council (SAFMC) in 1983 to conserve a population considered overexploited at that time (SAFMC and GMFMC[3]). The restrictions were enacted under the assumptions that cobia are widely dispersed, are primarily commercial bycatch, constitute a recreational fishery, and compose a single population in the United States. These restrictions were meant to reduce catches and allow females the opportunity to reproduce before entering the fishery. Data on regional fishing effort and catch indicate fishing pressure

[1] Burns, K. M., C. Neidig, J. Lotz, and R. Overstreet. 1998. Cobia (*Rachycentron canadum*) stock assessment study in the Gulf of Mexico and in the South Atlantic. Final Rep., MARFIN Coop. Agreement NA57FF0294 to NMFS (NOAA), 108 p. Mote Marine Laboratory, 1600 Thompson Parkway, Sarasota, FL 34236.

[2] NMFS (National Marine Fisheries Service.) 2012. Personal commun. Fisheries Statistics Division, Silver Spring, MD.

[3] SAFMC and GMFMC. 1983. Fishery management plan, final environmental impact statement, regulatory impact review, final regulations for coastal migratory pelagic resources (mackerels), 321 p. SAFMC, 4055 Faber Place, Suite 201, North Charleston, SC 29405.

for cobia has increased over the past decade (Steele[4]). Cobia continues to gain socioeconomic importance as a game fish throughout much of its range, supporting an expanding charterboat industry; however, the current status of this stock is unknown along the southeastern United States.

In spring and early summer, cobia in the western North Atlantic are thought to migrate along with warming waters from Florida to as far north as the mid-Atlantic Bight (Shaffer and Nakamura, 1989). During this presumed northward migration, cobia enter high-salinity bays and estuaries, including Port Royal Sound (PRS) and St. Helena Sound (SHS) in South Carolina, Pamlico Sound in North Carolina (Smith, 1996), and Chesapeake Bay (Shaffer and Nakamura, 1989), where they are readily available to inshore recreational anglers. Reasons for the inshore movement are not fully understood, but it is hypothesized that they may be following prey or aggregating to spawn.

On the east coast of the United States, the spawning season for cobia extends from April to September (Lotz et al., 1996; Smith, 1996; Burns et al.[1]; Brown-Peterson et al., 2001); the cobia is an indeterminate batch spawner with group-synchronous oocyte development and is capable of spawning multiple times during a season (Biesiot et al., 1994; Lotz et al., 1996; Brown-Peterson et al., 2001; van der Velde et al., 2010). Regional peaks in spawning, as designated by maxima in the gonadosomatic index (GSI), correlate with the migration of cobia from Florida northward. Spawning peaks along the Atlantic coast of the southeastern United States in May (Shaffer and Nakamura, 1989; Burns et al.[1]), off the coast of North Carolina in June (Smith, 1996), and in Chesapeake Bay in June and July (Joseph et al., 1964). In South Carolina, maximal spawning activity of cobia in May corresponds to peak fishing effort, as evidenced by increased landings during this month (Steele[4]). During the spring recreational fishery for cobia in South Carolina, cobia are easily accessible to anglers in the major coastal sounds, as they are in other states where they enter inland waters. Because the inshore migrations of this fish into PRS and SHS correspond with its spawning season, it is probable that these estuaries serve as spawning habitat.

Beyond a knowledge of spawning season, a paucity of information exists on spawning habitat and daily spawning periodicity of wild cobia, because much of the previous research on this species has focused on age and growth (Smith, 1996; Franks et al., 1999), feeding habits (Smith, 1996; Arendt et al., 2001), and general reproductive biology (Biesiot et al., 1994; Lotz et al., 1996; Smith 1996; Brown-Peterson et al. 2001; van der Velde et al. 2010). Hassler and Rainville (1975) collected eggs in the Gulf Stream off North Carolina and suggested that spawning took place offshore. Burns et al.[1] also proposed offshore spawning because of a scarcity of fish with histological signs of final oocyte maturation (FOM) collected in nearshore waters of the Gulf of Mexico and the Atlantic coast of the southeastern United States. It has been proposed that inshore spawning of cobia occurs in the lower Chesapeake Bay on the basis of egg collections immediately south of this bay (Joseph et al., 1964) and the ovarian condition of females collected in this bay (Richards, 1967). In North Carolina, Smith (1996) suggested that cobia spawned adjacent to inlets, on the basis of the presence of eggs in neuston net collections within inlets and a lack of females caught inshore that were undergoing FOM. Additionally, Ditty and Shaw (1992) reported eggs and larvae from another high-salinity bay, Crystal Bay, Florida.

Our objective was to determine whether cobia spawn within 2 high-salinity estuaries in South Carolina, PRS and SHS. Histological analysis of ovarian tissue collected in 2007 and 2008 was used to evaluate the reproductive status of female cobia caught in the recreational fishery both inshore and offshore of these estuaries. A study of egg development conducted in 2007 and 2008 with hatchery-reared cobia eggs provided embryological development characteristics and insight on time of day of spawning for wild cobia. An ichthyoplankton survey targeting cobia eggs and larvae in PRS and SHS was conducted during the 2008 spawning season to provide additional evidence of spawning locations. We discuss the results of this project, particularly with respect to the occurrence of springtime inshore aggregations of cobia, in light of the increasing fishing pressure cobia are experiencing and in regard to current management regulations.

Materials and methods

Fish collections and reproductive biology

Fresh and frozen cobia specimens from PRS and SHS, South Carolina (Fig. 1), were collected by members of the Estuarine Finfish Research Group at the South Carolina Department of Natural Resources (SCDNR) at fishing tournaments and from cooperating anglers, recreational fishing guides, and employees of the SCDNR during the period from April to June in both 2007 and 2008. Specimens were measured for total length (TL, millimeters) and fork length (FL, millimeters) and weighed (fish weight [FW]) to the nearest kilogram. Sex was determined macroscopically, and gonads were excised, stored on ice, and transported to the SCDNR Marine Resources Research Institute (MRRI; Charleston, SC). Date, time, and location of capture were noted when available: fish collected within PRS and SHS were designated as "inshore" specimens, and those fish collected in the ocean beyond the barrier islands were designated as "offshore" specimens. Some cobia carcasses were accumulated in freezers located at marinas and tackle stores: anglers donated the carcasses after filleting, and the aforementioned information was voluntarily recorded.

At the MRRI, gonads were weighed to the nearest gram, and the GSI was calculated:

[4] Steele, G. 2009. Personal commun. South Carolina Department of Natural Resources, Charleston, SC 29412.

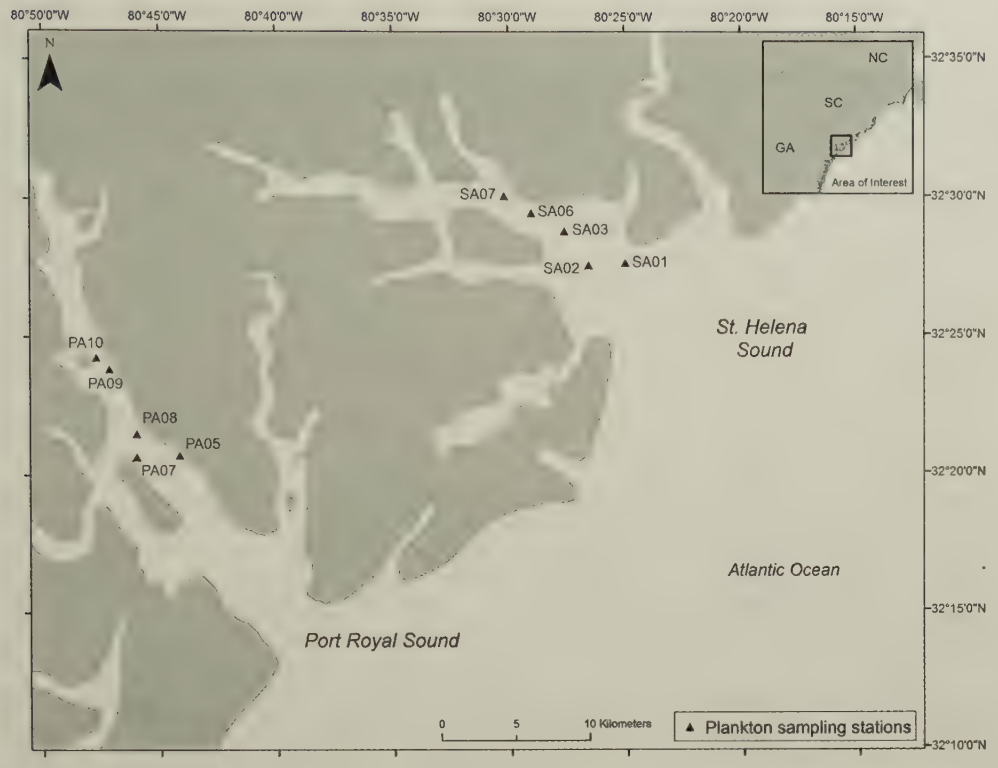

Figure 1

Coastal South Carolina and estuaries that cobia (*Rachycentron canadum*) enter during their annual northward spring migration. For this study of inshore spawning, cobia were collected from 2 inshore estuaries, Port Royal Sound and St. Helena Sound, and offshore in 2007 and 2008. Triangles indicate stations sampled in each estuary during the ichthyoplankton survey conducted in 2008. Map by Jessica Boyton (South Carolina Department of Natural Resources).

$$GSI = \left(GW/SW\right) \times 100,$$

where GW = gonad weight (grams); and
SW = somatic weight (grams).

To determine whether GSI values for male and female cobia were significantly different, a Wilcoxon rank test was performed. To evaluate if ovarian maturation differed between inshore and offshore collections of female cobia, a Wilcoxon rank test was performed with the GSI as a proxy for maturation for statistical purposes. Nonparametric Wilcoxon tests were performed because the data displayed non-normality, which resulted from the capture of 2 actively spawning females. A t-test was used to determine if differences in GSI between inshore and offshore females persisted after exclusion of the GSI values from the 2 actively spawning females.

Histological analyses were limited to samples collected from female cobia because males are capable of spawning year-round (Brown-Peterson et al., 2001). Homogenous ovarian development has been documented previously for cobia (Lotz et al., 1996; van der Velde et al., 2010); therefore, a single portion of tissue (~50–100 mg) from the middle of one ovarian lobe was fixed in 10% neutral buffered formalin before being rinsed in freshwater and stored in 50% isopropyl alcohol at least 24 hr before processing. Tissue samples were dehydrated, infiltrated and blocked in paraffin, sectioned to 6 µm with a rotary microtome, mounted on glass slides, and stained with hematoxylin and eosin-y according to standard histological techniques (Humason, 1972). Slides were examined under a compound microscope at 100× magnification and staged according to ovarian development. Ovarian phases (Table 1) were determined on the basis of descriptions of teleost oocyte development in Wallace and Selman (1981), with modifications from Roumillat and Brouwer (2004) and Brown-Peterson et al. (2011). When present, postovulatory follicles (POFs) were categorized as either less than or equal to or greater than 12 hr old, on the basis of rates of POF atresia found in spotted seatrout (*Cynoscion nebulosus* [Roumillat and Brouwer, 2004]). Vitellogenic oocytes of specimens that had been frozen or had begun to decay before collection superficially resembled oocytes at the beginning stages of FOM, with nucleus migration and early lipid coalescence. To avoid confusion between FOM and damaged tissue, FOM stages earlier than the hydration stage were not addressed. All samples were staged by a second, independent reader. All discrepancies were resolved by both readers simultaneous view-

Table 1

Stage of ovarian development was determined for female cobia (*Rachycentron canadum*) collected during the period from April to June in both 2007 and 2008 for this study of inshore spawning of cobia in South Carolina. Phases were based on descriptions of teleost oocyte development by Wallace and Selman (1981) and modified from Roumillat and Brouwer (2004) and Brown-Peterson et al. (2011). FOM=final oocyte maturation; POF=postovulatory follicle.

Phase	Subphase	Description
Immature		Only oogonia and primary oocytes present. Fish has not yet reached sexual maturity and is incapable of spawning.
Developing		Primary growth oocytes dominate. A few early vitellogenic oocytes may be present and are <500 µm in diameter. Cortical alveoli visible. On the basis of diameter, there is a dominant batch of small vitellogenic oocytes and a few larger vitellogenic oocytes. Fish has not yet spawned this season.
Spawning capable	Late developing	Primary growth, cortical alveolar, early vitellogenic and advanced vitellogenic oocytes present, with the diameter of oocytes in the largest batch at 500–850 µm. On the basis of diameter, there are at least 2 distinct batches of vitellogenic oocytes. Some atresia may be present. Fish is capable of spawning and may have previously spawned.
	Actively spawning	One batch of oocytes undergoing FOM (through hydration), as evidenced by lipid coalescence and a diameter >850 µm. More advanced stages of FOM also will show migration of nucleus to animal pole. Oocytes in the next-largest batch are 300–500 µm in diameter. Spawning imminent.
	Past spawner 1—recent spawning	Recent POFs are abundant and distinguished by size (>250 µm across longest axis) and morphological features. Recent POFs are amorphous and clearly show multiple infoldings of thecal and granulose cells Oocytes in the largest batch are 300–550 µm in diameter. Fish has spawned within 0–24 hr.
	Past spawner 2—previous spawning	Degradation of POFs indicates spawn was >24 hr prior. Older POFs are triangular in shape, condensed, and less numerous compared with recent counterparts. Oocytes in the largest batch are 550–700 µm in diameter.
Regressing		Majority of largest batch of vitellogenic oocytes undergoing atresia. Oogonia and primary growth oocytes may be present. This stage is indicative of cessation of spawning for the season.
Regenerating		Oogonia and primary growth oocytes dominate. Other oocytes are in late stages of atresia.

ing the questionable slides. Percent composition (PC) of females in each of the ovarian maturation phases was calculated separately for females collected inshore and for females collected offshore:

$$PC = \left(n_s / T\right) \times 100,$$

where n_s = the number of female samples in phase s; and
T = the total number of samples.

Egg-development study

Identification and aging of candidate eggs from the plankton collections were accomplished by using a time-series reference collection of cobia eggs obtained from wild-caught adult cobia spawned in the laboratory in 2007 and 2008 for the egg-development study described below. Cobia yolksac larvae from the egg-development study in 2007 served as reference for the identification of young larvae in the plankton collections. The temperature treatments during the egg-development study of hatchery-reared eggs fell within the measured range of surface temperatures (20.1–30.0°C) encountered in PRS and SHS during May and June of both years (2007–2008).

In 2007 at the Hollings Marine Laboratory in Charleston, South Carolina, 4 fiberglass hatching cones (170 L) were equipped with aerators and heaters and filled with seawater (34.5 psu) from Charleston Harbor that had been filtered (5 µm) and UV-sanitized after settling for 3 days. The water in these cones was heated to 22.5°C, 25.0°C, 26.5°C, and 29.0°C, respectively, and

maintained for 48 hr before the start of this study. Four 50-mL aliquots of eggs (~2×10^4 eggs) were used in the trial. Before the addition of eggs to the water baths at ~11 hr postspawn, digital micrographs of eggs were recorded with a Nikon[5] SMZ1500 stereo microscope (Nikon Instruments, Inc., Melville, NY) mounted with a Micropublisher 3.3 camera (QImaging, Surrey, BC, Canada). Thereafter, ~10 eggs or larvae were collected from each tank, and micrographs were recorded every 4 hr until 61 hr after spawning. After images were recorded, eggs and larvae were preserved in 10% neutral buffered formalin.

To capture earlier stages of egg development and to expand the range of experimental temperatures, we expanded the egg-development study in 2008. Three water baths were heated to and maintained at 24.0°C, 26.0°C, and 28.0°C in a temperature-controlled laboratory 30 hr before the beginning of this second study. Two hours after time of spawning, a 25-mL aliquot of cobia eggs (~1×10^4 eggs) was divided between petri dishes in each temperature bath. Every hour, until 13 hr after spawning, and every other hour thereafter up to 25 hr after spawning, a sample of ~10 eggs was removed from each water bath, digital micrographs were recorded, and eggs were preserved in 10% neutral buffered formalin.

Micrographs of live eggs were taken, and both egg diameters and oil-droplet diameters were measured to the nearest micrometer by using ImageJ image-analysis software (vers. 1.38, ImageJ, Bethesda, MD). To determine if damage and diameter changes occurred with preservation, changes in appearance were noted, and measurements of egg and oil-droplet diameters were measured to the nearest micrometer from micrographs of preserved eggs taken ~1 year from the date of collection in 2007 and 2 months from the date of collection in 2008. Diameters were measured only for undamaged, preserved eggs. Percent shrinkage was calculated as the change in egg and oil-droplet diameters between the live and corresponding preserved eggs multiplied by 100. To determine if a significant decrease in diameter because of preservation had occurred, 2-sample *t*-tests were performed independently for 2007 egg and oil-droplet diameters and 2008 egg diameters. Because of non-normality of the 2008 oil-droplet-diameter data, a Wilcoxon rank test was performed with these data to determine if significant shrinkage had occurred after preservation.

With the use of the micrographs of live eggs from the egg-development studies, coarse stages of embryological development were described. Because the earliest stages of egg development were captured only in the 2008 study and larvae hatched only in the 2007 study, the 2 temperature treatments that were closest in temperature (26.5°C in 2007 and 26°C in 2008) were used for the characterization of egg-development stages from the earliest ones to the hatching stage.

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Ichthyoplankton survey

Field collections Five stations in each of the 2 estuaries (Fig. 1), located in known cobia fishing grounds, were sampled weekly from 6 May to 15 June 2008 in PRS and 8 May to 8 June 2008 in SHS. Collections occurred between 0745 and 1945 hr. Survey stations in PRS were located 12.1 to 20.6 km inshore from the mouth of that estuary. Stations in SHS were located 5.1 to14.3 km inshore from the mouth of that estuary. Stations were positioned upriver of particular bathymetric features where anglers typically target cobia. These stations were adjacent submerged sand bars and banks where water depths rose from 10 to 12 m at mean low water to 2 to 3 m at mean low water. Depths of stations ranged from 5.5 to 9.6 m at the time of net deployment. Anchored plankton nets, made of Nitex nylon mesh (Sefar Holding AG, New York, New York), were deployed at slack water before the daylight flood tide. These plankton nets had a mouth 0.5-m in diameter and were 2.5 m long, with a mesh size of 505 µm along the length and 303 µm at the codend. Floats attached to circular frames maintained the position of these nets at ~1 m below the surface. Flow meters were mounted in the center of these nets at the most seaward and farthest inshore stations. At the time of net deployment, ancillary water data were collected (temperature, salinity, dissolved oxygen) at the surface and bottom of the water column with a handheld instrument, YSI 556 MPS (YSI, Inc., Yellow Springs, Ohio). Plankton nets were deployed for the length of time required to set all nets and return to retrieve the first one (70–150 min). The average current speed during the time of collection was calculated by using the flow meter readings. Volume of water filtered was calculated directly from flow meter readings in nets. For nets without flow meters, current speeds and volumes filtered were estimated by averaging the values from the most seaward and farthest inshore stations.

Egg and larval identification Plankton samples were rinsed and then sorted under a dissecting microscope. When settled plankton volumes were greater than 1 L, samples were split with a Burrell plankton splitter (Burrell et al., 1974) until a settled plankton volume of 0.5 L or less was attained. All nonclupeiform larvae were removed, identified to lowest possible taxonomic level (Moser et al., 1984; Richards, 2005), and preserved in 70% isopropyl alcohol. Cobia larvae were identified from descriptions of Ditty and Shaw (1992). All eggs measuring between 1.0 and 1.4 mm with an ocular micrometer and having one or more of the morphological characteristics corresponding to cobia eggs—single, large (300 to 600 µm), pigmented oil droplet, heavily pigmented embryo, or narrow perivitelline space (Ditty and Shaw, 1992; Ditty, 2006)—were removed and preserved in 10% neutral buffered formalin.

Digital micrographs of preliminarily identified cobia eggs were recorded. Diameters of all eggs and of single, intact oil droplets from preserved eggs were measured to the nearest micrometer with ImageJ. To aid in iden-

tification, eggs from the 2 development studies were viewed as references. Eggs were positively identified as cobia if their diameter fell within the range noted in the literature (1.0–1.4 mm) and if the morphological characteristics, with the exception of number and diameter of oil droplets, matched the hatchery-reared eggs and published description of cobia eggs (Ditty and Shaw, 1992; Ditty, 2006). The number and diameter of oil droplets were excluded as positive identifying characters because of damage incurred during preservation. For further analyses, eggs were labeled as early stage or late stage. The early stage comprised eggs from fertilization to blastopore closure, with the embryo not visible in preserved eggs (Ahlstrom and Moser, 1980). The late stage comprised eggs from blastopore closure to hatching, with the embryo evident in preserved eggs, including eggs at mid and late stages as described in Ahlstrom and Moser (1980).

For secondary evidence for correct identification of eggs, an analysis of covariance (ANCOVA) was conducted to test for differences in the relationship of egg and oil-droplet diameters between known cobia eggs (early and late-stage eggs from the 2007 and 2008 egg-development studies) and eggs identified from plankton samples. If the relationship was not significantly different between hatchery-reared and field-collected eggs, the field-collected eggs were confirmed as cobia. Only measurements from eggs with single, intact oil droplets were used in the ANCOVA.

For plankton samples that contained more than one undamaged egg, ages of cobia eggs were estimated through side-by-side comparison to eggs reared at the closest matching temperature from either the 2007 or 2008 development study. In early-stage eggs that turned opaque with preservation, it was difficult to discern their stage of cell division or cleavage; therefore, age was estimated only for eggs that were not opaque. For a given sample, time of spawning was approximated on the basis of the age of an egg, which was estimated by back-calculating from the time of sample collection. When field-collected eggs resembled an intermediate stage between 2 sampling time periods within the egg development study, ages were estimated to be halfway between the 2 periods. Numbers of cobia eggs and larvae from split samples were estimated from the fraction of the sample sorted. Concentrations of cobia eggs and larvae collected in the ichthyoplankton survey were obtained by using calculated and estimated sample volume filtered for the corresponding sample.

All statistical analyses were conducted using R statistical software (R Development Core Team, 2009). The significance level of α=0.05 was used for all tests.

Results

Between April 2007 and June 2008, 554 cobia (275 females, 279 males) were collected. Of these fish, 262 came from carcass donations, 261 from fishing tournaments, and 31 from SCDNR. Specimens ranged in size from 850 to 1425 mm FL (mean=1042 mm) for females and 386 to 1215 mm FL (mean=930 mm) for males. Weights ranged from 6.7 to 38.3 kg (mean=15.0 kg) for females and 0.5 to 23.0 kg (mean=9.9 kg) for males. Most of the largest fish were female: 80% of the fish 1000 mm FL or longer and 79% of the fish 10 kg or greater in total weight. Capture locations were available for 183 fish (44 offshore, 101 PRS, 39 SHS).

Reproductive biology

GSIs were calculated for 278 cobia (164 females, 114 males) and were combined for April, May, and June of both years because of small sample sizes collected in April and June. GSI for all cobia ranged between 0.7 and 22.5 (mean=6.1), and females had a significantly higher mean GSI (7.3) than males (4.4; P<0.05). Ovarian growth in other group-synchronous, batch-spawning species is isometric with body growth (Taylor et al., 1998; Somarakis et al., 2004), and previous work on cobia ovaries with FOM has shown that there is no relationship between relative fecundity and either body weight or fork length (Brown-Peterson et al., 2001; van der Velde et al., 2010); therefore, female GSI was deemed appropriate as a proxy for ovarian maturation for statistical purposes. The average GSI from females collected inshore (mean=7.8; n=64) was significantly higher than the average GSI from females collected offshore (mean=5.6; n=34; p=0.002), indicating that ovaries were in a more developed state in inshore fish than in offshore fish. The mean inshore GSI (7.4) remained statistically higher than the mean offshore GSI (5.6; P=0.003) with removal of the actively spawning females. Therefore, the higher mean GSI from females collected inshore was not biased by the collection of actively spawning females inshore or spent females offshore.

Histological analysis of 213 ovaries showed that female cobia were in the middle of their reproductive season and capable of spawning during May and June. All ovarian phases, except the immature and regenerating phases, were represented in the female samples examined (Fig. 2). Immature specimens were unavailable because current fishing regulations impose a minimum FL (84 cm), which is larger than the approximate length at first maturity for female cobia (80 cm). Females in the regenerating state were likely absent because sampling was done during the spawning season.

Further histological analysis of female ovarian samples was limited to 98 specimens for which capture location was known (64 inshore and 34 offshore). The majority (72%) of female cobia collected from both inshore and offshore waters had ovaries in the late development subphase of the spawning capable phase (Table 2). Two females with ovaries in the developing phase were collected offshore in early April 2007 and inshore in early May 2007. Both of these females (89 cm FL and 93 cm FL, respectively) were larger than the typical size at maturity, had no evidence of prior spawning (POFs), and were, therefore, likely maturing

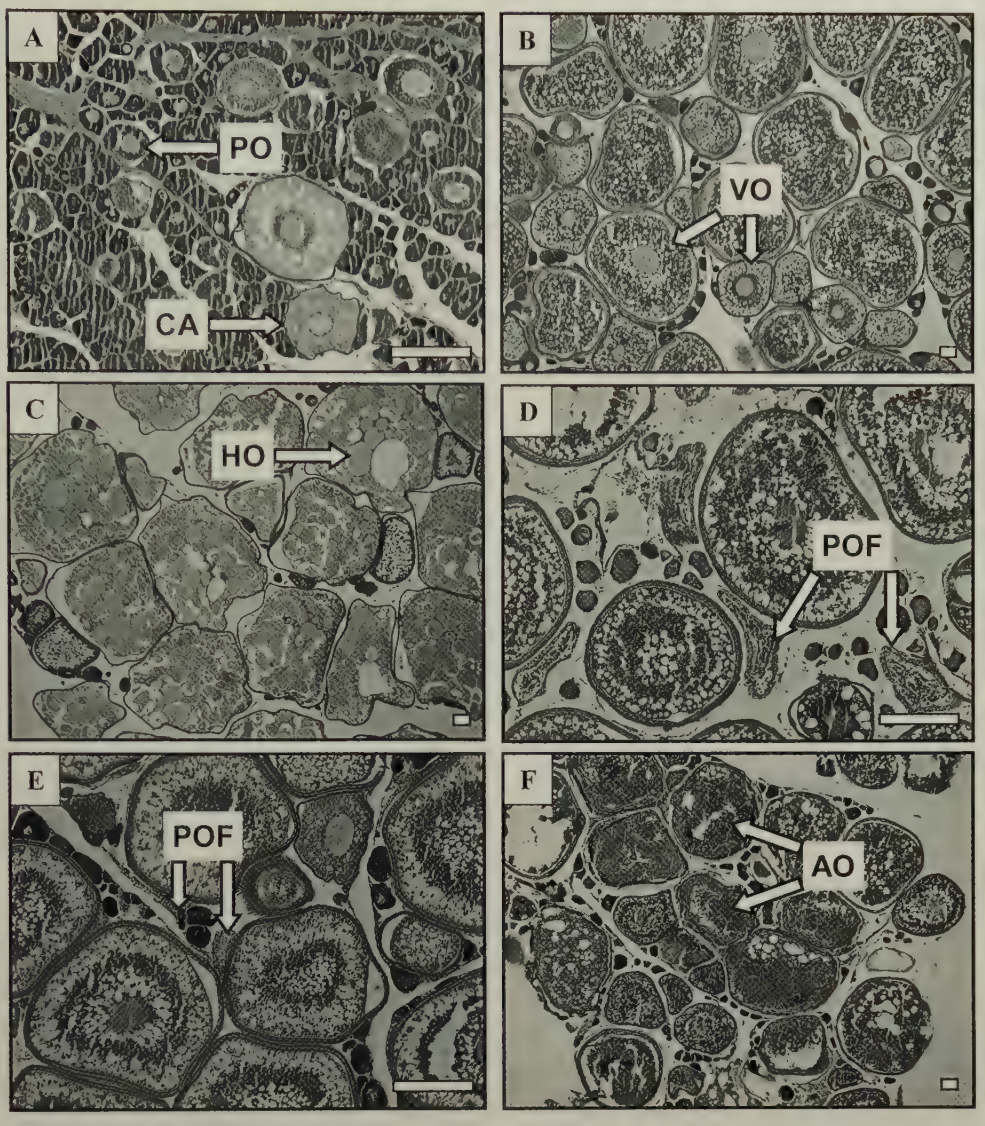

Figure 2

Histological micrographs of the ovarian phases of cobia (*Rachycentron canadum*) collected in South Carolina waters in 2007 and 2008. Scale bars=200 µm. (**A**) Developing: primary oocytes (PO) dominate with few cortical alveolar (CA) present. Spawning capable: (**B**) late developing (subphase): vitellogenesis continues; multiple batches of vitellogenic oocytes (VO) are present; (**C**) actively spawning (subphase): hydrated oocytes (HO) show lipid coalescence; (**D**) past spawner 1—recent spawning (subphase): most recent postovulatory follicles (POF) are 250 µm across longest axis; multiple batches of VO present; and (**E**) past spawner 2 (subphase)—previous spawning: POF are less numerous and are smaller, more condensed, and triangular in shape; multiple batches of VO present. (**F**) Regressing: largest batch of VO are undergoing atresia (AO).

for the first time in this spawning season. A single female in the regressing phase was collected in offshore waters in early June 2008. Females with histological signs of previous spawning (visible POFs) were found in cobia collected inshore and offshore. All POFs were estimated to be greater than 12 hr old (Hunter and Macewicz, 1985; Roumillat and Brouwer, 2004), with the exception of one specimen collected during morning hours in May 2007, for which the POFs were estimated to be ~12 hr old.

Two actively spawning females were collected from inshore waters in 2007. The first (121.6 cm FL and 27 kg FW) was collected in mid-morning on 12 May in the Broad River (PRS). The second (93.4 cm FL and 11

Table 2

State of ovarian development of female cobia (*Rachycentron canadum*) collected during the period from April to June in both 2007 and 2008 for this study of inshore spawning of cobia in South Carolina. No.=number of fish; PC=percent composition.

		Inshore		Offshore		Unknown	
Phase	Subphase	No.	PC	No.	PC	No.	PC
Immature		0	0	0	0	0	0
Developing		1	2	1	3	1	1
Spawning capable	Late developing	51	80	20	59	97	84
	Actively spawning	2	3	0	0	3	3
	Past spawner 1—recent spawning	3	5	1	3	4	4
	Past spawner 2—previous spawning	7	11	11	32	9	8
Regressing		0	0	1	3	1	1
Regenerating		0	0	0	0	0	0

kg FW) was caught by SCDNR employees in SHS on 8 June at 1030 hr. Both had ovaries in the late stage of FOM, during which yolk coalescence and hydration occurs immediately before ovulation. The time of collection, state of oocyte hydration, and rapid nature of FOM found in other multiple-spawning species with similar geographic distributions (Brown-Peterson et al., 1988; Fitzhugh et al., 1993; Roumillat and Brouwer, 2004) indicate that these 2 specimens would have spawned the afternoon of capture.

Egg-development study

Micrographs of cobia eggs from the 2007 and 2008 development studies of hatchery-reared eggs were taken at 13 and 19 sampling times, respectively. In 2007, eggs hatched between 39 and 43 hr postspawning at 22.5°C; between 29 and 33 hr at 25.0°C; and between 25 and 29 hr at 26.5°C. Eggs incubated at 29°C were observed hatching 26 hr after having been spawned as micrographs were being recorded. At the end of the study in 2007, all larvae still had yolk sacs and were 3.8 to 4.6 mm TL. The 2008 development study ended before any eggs hatched. Mean egg diameters of live cobia eggs were 1241 and 1337 µm in 2007 and 2008, respectively. Mean oil-droplet diameters were 359 µm in 2007 and 403 µm in 2008.

Micrographs of preserved eggs from each year revealed damage to the oil droplet in many specimens because of preservation or handling (Fig. 3). Irregularly shaped oil droplets occurred most often in early-stage eggs. Damage in late-stage eggs included split oil droplets or droplets in which the pigmented portion had detached from the lipid (Fig. 3B). Measurements of preserved eggs were limited to specimens that had a single, intact oil droplet. The mean egg diameter of preserved eggs from both years was 1280 µm, and the mean diameter of oil droplets was 380 µm. The average diameters of eggs and oil droplets for both preserved and live cobia eggs fell within the published range (Table 3 [Ditty and Shaw, 1992; Ditty, 2006]). Upon preservation, cobia eggs shrank significantly: 1.7% in 2007 ($P<0.05$) and 1.0% in 2008 ($P<0.05$). No shrinkage occurred in the diameters of oil droplets during either year (2007, $P=0.13$; 2008, $P=0.92$).

Five stages of embryological development were described for cobia (Fig. 4) and are detailed below. Duration of each stage was approximated in hours. Overlap was observed in the durations of stages III and IV because of minor differences between eggs in the 2007 and 2008 development studies.

Stage I (0–7 hr; Fig. 4, A and B): newly fertilized eggs had a distinct, translucent oil droplet. Early cell divisions were evident at the animal pole (opposite of the oil droplet) and eventually formed the blastodisc. Divisions progressed until individual blastomeres were no longer distinguishable. Stage I ended when the germ ring was visible and enclosed approximately one-third of the yolk mass.

Stage II (7–13 hr; Fig. 4C): the germ ring became distinct and epiboly proceeded until the germ ring was in center of the egg. Stage II ended when the blastopore was closed and the optic cups distinguished head and tail regions of the embryo.

Stage III (13–19 hr; Fig. 4D): the embryo was greater than one-quarter of the internal circumference of the egg. Somites were distinct. Stellate melanophores were scattered around the outside of the yolk. Pigmentation on the embryo increased (from head towards anterior of caudal region). Stage III ended with first appearance of melanophores on the oil globule and when the embryo was approximately one-half the internal circumference of the egg.

Stage IV (14–21 hr; Fig. 4E): the embryo continued to become more heavily pigmented. "Free" melanophores continued to congregate on the oil globule until there were few to no free melanophores around the outside

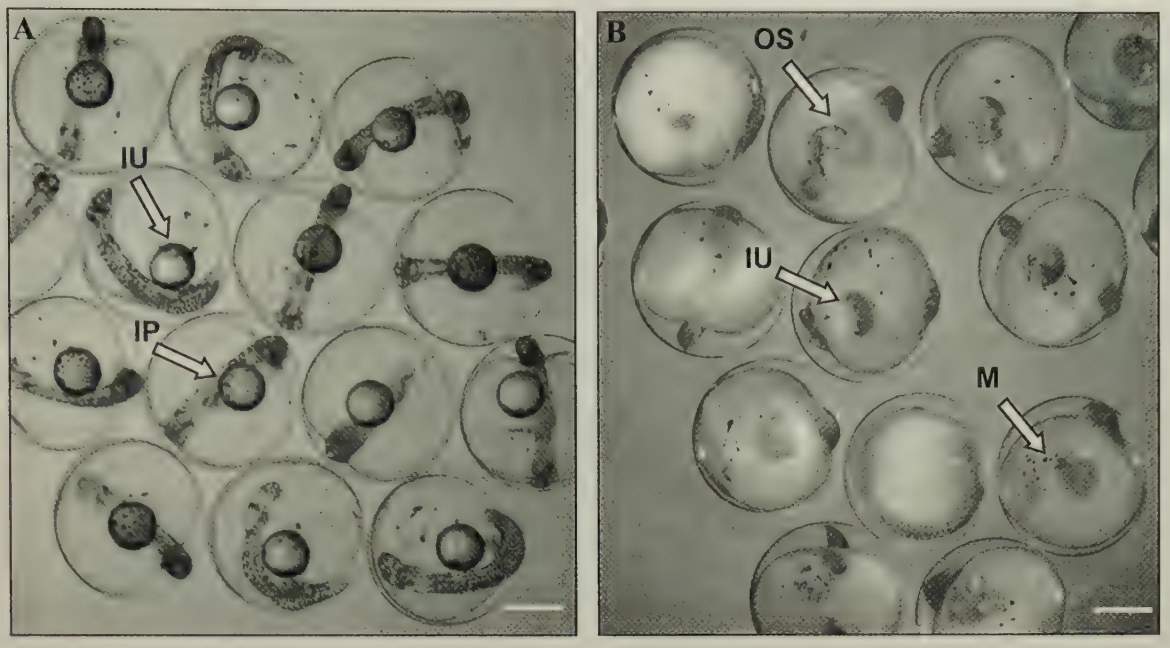

Figure 3

Micrographs of late-stage hatchery-reared cobia (*Rachycentron canadum*) eggs from the egg-development study conducted in 2008. Scale bars=500 µm. (**A**) 21-hr-old eggs before preservation. IU=intact oil droplet (OD), unpigmented; IP=intact OD, pigmented. (**B**) The same eggs after 2 months in 10% neutral buffered formalin. OS=oil separating from pigmented portion; M=multiple OD.

Table 3

Descriptions of cobia (*Rachycentron canadum*) eggs from hatchery-reared eggs, eggs collected in plankton samples in 2008, and from Ditty (2006). Asterisks (*) indicate that only eggs with a single oil droplet were measured.

	Hatchery		Plankton samples	
Parameter	Live	Preserved*	Preserved*	Literature
Diameter	1.21–1.38 mm (mean: 1.30 mm)	1.18–1.37 mm (mean: 1.29 mm)	1.15–1.39 mm (mean: 1.28 mm)	1.15–1.42 mm (mean: 1.24 mm)
Number of oil droplets	1	1 to several, often irregular in shape	1 to several, often irregular in shape	1
Oil-droplet diameter	0.34–0.42 mm (mean: 0.38 mm)	0.32–0.42 mm (mean: 0.38 mm)	0.28–0.42 mm (mean: 0.36 mm)	0.34–0.65 mm (mean: 0.45 mm)
Oil-droplet pigment	present	present; in some eggs, pigment separated from oil	present; in some eggs, pigment separated from oil	present
Perivitelline space	narrow	narrow	narrow	narrow
Embryonic pigment	heavy, except on caudal peduncle	heavy, except on caudal peduncle	heavy, except on caudal peduncle	heavy, except on caudal peduncle

of the yolk. The embryo began to move, as evidenced by flexion of the body. Stage IV ended when the tail was visibly detached from the yolk and the embryo was approximately three-quarters the internal circumference of the egg.

Stage V (21–29 hr; Fig. 4F): the embryo continued to become more heavily pigmented. More movement of the embryo was evident. The embryo was greater than 100% the internal circumference of the egg before hatching, with the tail extending beyond the head.

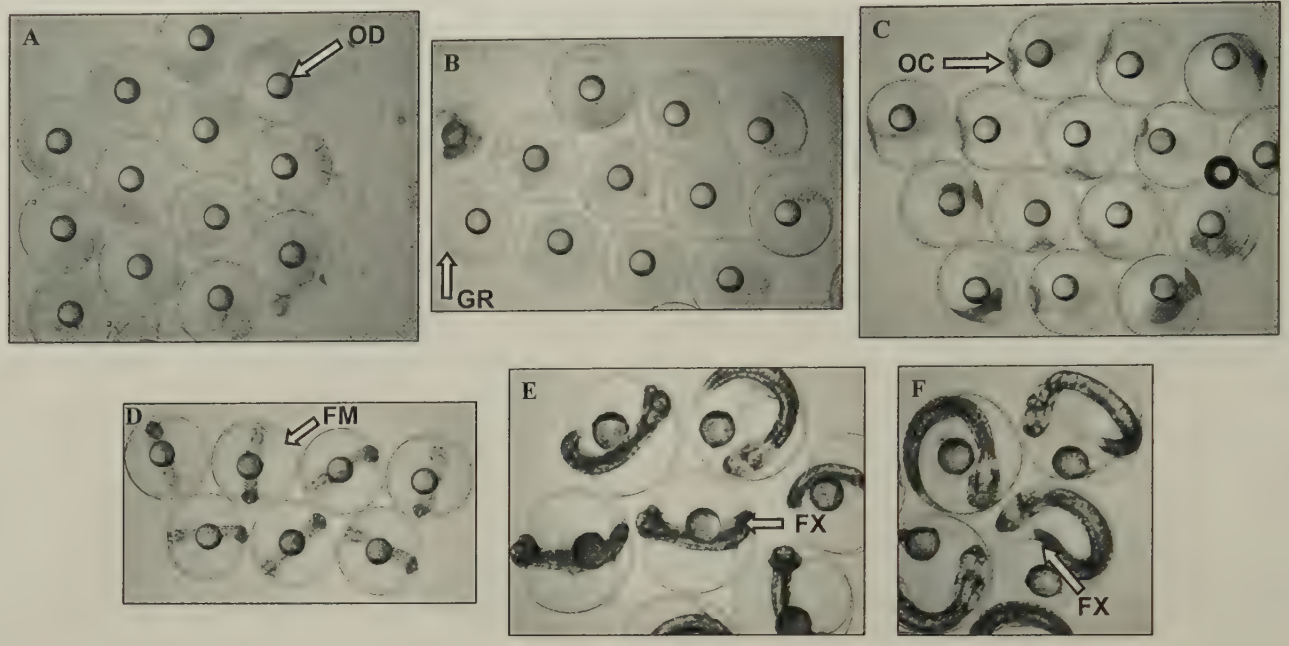

Figure 4

Micrographs of embryonic development of cobia (*Rachycentron canadum*) eggs (A, B, C, and D) from the 2007 egg-development study of hatchery-reared eggs (26.5°C) at 20× magnification and of eggs (E and F) from the 2008 development study (26°C) at 40× magnification. (**A**) Stage I (1 hr postfertilization [pf]): newly fertilized egg with single oil droplet (OD) and first cellular divisions occurring. (**B**) End of stage I, start of stage II (7 hr pf): germ ring (GR) has formed. (**C**) Stage II (13 hr pf): optic cups (OC) distinguish head and tail regions of embryo. (**D**) Stage III (17 hr pf): embryo is acquiring pigmentation, and somites are visible; free melanophores (FM) in yolk begin to migrate toward OD. (**E**) Stage IV (21 hr pf): embryo is heavily pigmented and is >50% the internal circumference of the egg; flexion (FX) of embryo is evident. (**F**) Stage V (25 hr pf): embryo fills more of the egg and greater movement is evident.

Ichthyoplankton survey

Between 6 May and 18 June 2008, 52 anchored plankton-net samples (26 PRS, 26 SHS) were collected. All samples from PRS were sorted completely. Of the 26 samples from SHS, 17 were split to one-half (1 sample), one-quarter (14 samples), or one-eighth (2 samples) the original volume. Measured current speeds ranged from 0.08 to 0.93 m/s (0.29 to 3.35 km/hr), and most speeds ranged between 0.14 and 0.71 m/s (0.50 to 2.56 km/hr). Volumes filtered through the plankton nets ranged from 120 to 1156 m^3. Surface water temperatures in both estuaries ranged from 20.1°C to 30.0°C. Salinities ranged from 31.6 to 34.3 psu in PRS and from 28.4 to 32.7 psu in SHS; these values are within tolerable ranges for larval, juvenile, and adult cobia (Hassler and Rainville, 1975; Shaffer and Nakamura, 1989; Denson et al., 2003). The water columns in both PRS and SHS were well mixed, with little variation of surface and bottom temperatures and salinities (±0.8°C and 0.8 psu, respectively).

On the basis of size and morphological characteristics, 926 eggs were identified as cobia (562 early stage and 364 late stage [Tables 3 and 4; Fig. 5]). Late-stage eggs occurred in samples collected at all stations in PRS (59 eggs). At a single station (PA08) ~15 km inshore, 27 early-stage eggs from PRS were collected at 1930 hr on 5 June 2008 (Table 4). The majority of the eggs identified as cobia were from SHS, with 535 early-stage eggs and 305 late-stage eggs collected among all stations. Of the early-stage eggs found in SHS, 496 came from a single sample collected at 1900 hr on 3 June 2008 at a station (SA03) ~9.7 km inshore (Table 4). Late-stage eggs were collected between 1230 and 1945 hr in both estuaries on 8 sampling days. Egg concentrations ranged from 0.14 to 62.51 eggs/100 m^3 (Table 4).

Egg diameters ranged from 1116 to 1393 µm (mean=1292 µm). The diameters of 73 intact oil droplets ranged from 275 to 420 µm (mean=357 µm). The mean diameters of eggs and oil droplets were similar to the diameters observed for hatchery-reared cobia eggs and to diameters reported elsewhere (Table 3) (Ditty and Shaw, 1992; Ditty, 2006). Measurements of early- (48 eggs) and late-stage (25 eggs) eggs were combined for the ANCOVA. Because of egg shrinkage, only measurements from preserved hatchery-reared eggs were used for the ANCOVA. The mean diameter of oil droplets for field-collected eggs (357 µm) was lower than the mean for hatchery-reared cobia eggs (380 µm); however, the

ANCOVA showed that the slopes of the regression lines were not statistically different (P=0.35; overall coefficient of determination [r^2]=0.61; Fig. 6). This result supports our visual identifications of cobia eggs in the plankton collections.

Most early-stage eggs turned opaque: ages were estimated from a single sample collected 5 June 2008 in PRS, and eggs were ~2–3 hr old. The ages of late-stage eggs were estimated at between 18 and 26 hr old. Time of spawning was estimated to range from the late afternoon (1530 hr) to late evening (2145 hr), and most spawning occurred between 1530 and 1800 hr (Table 5). The 3 exceptions were from one day in SHS, when spawning probably occurred near midnight. Although age estimates of the field-collected eggs were admittedly subjective, eggs collected from multiple stations on the same day were aged independently, and all of them were estimated to be nearly the same age.

Over 8 sampling days, 42 cobia larvae (18 PRS; 24 SHS) were collected. Larval concentrations ranged between 0.17 and 1.99 larva/100 m^3 (Table 5). Five yolksac cobia larvae were collected: 2 on 14 May 2008 (stations PA05 and PA08), 1 on 29 May 2008 (station PA07), and 2 on 21 May 2008 (station SA01).

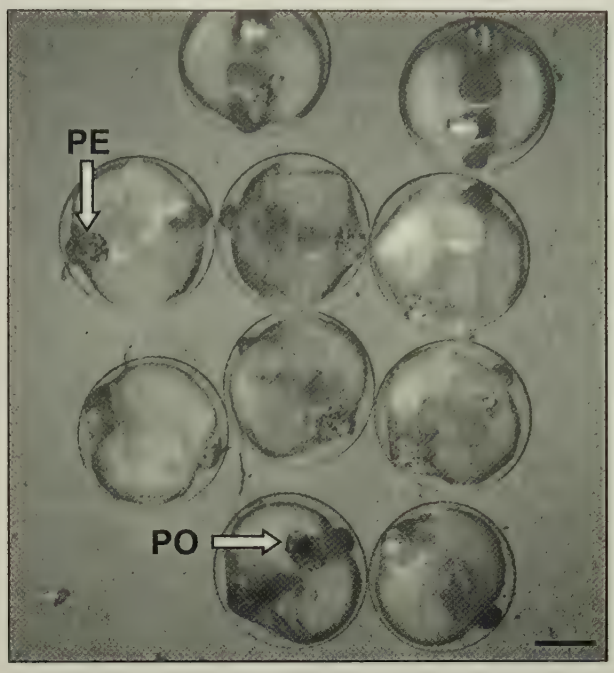

Figure 5

Micrograph of late-stage cobia (*Rachycentron canadum*) eggs collected from ichthyoplankton surveys conducted in Port Royal Sound, South Carolina, on 29 May 2008. PO=pigmented oil droplet; PE=pigmented embryo. Scale bar=500 µm.

Discussion

The results of this study indicate that cobia spawn within PRS and SHS, South Carolina, as evidenced by the high mean GSIs of females, the collection of actively spawning females, the presence of recently fertilized eggs, and the presence of larvae in these 2 estuaries. Through the use of the estimated ages of field-collected eggs, in combination with time and location of capture from adult cobia collected at fishing tournaments, this study provides evidence of spawning of wild cobia in estuarine waters in the late afternoon and early evening hours.

The mean GSI of female cobia collected in this study peaked at a higher value (7.3) than was previously reported for cobia in the Gulf of Mexico by Biesiot et al. (1994; 5.5), Lotz et al. (1996; 5) and Brown-Peterson et al. (2001; 4.5); in North Carolina by Smith (1996; 5.7); and along the Atlantic coast of the southeastern United States by Brown-Peterson et al. (2001; 5.5). The higher mean GSI value reported in this study is not biased by the collection of 2 actively spawning females: when these females were removed from analyses, the mean GSI values were still well above the values reported elsewhere. In addition to a higher GSI value, the size range of oocytes (500–850 µm) in ovaries in the late developing subphase (the phase that dominated collections in this study) was greater than the size range reported elsewhere for the group with the most developed oocytes (500–650 µm [Lotz et al., 1996]). Fully developed and fertilized cobia eggs in this study and in Ditty and Shaw (1992) ranged in size from 1.15 to 1.42 mm; therefore the larger oocyte sizes found in developing ovaries suggest that oocytes were more highly developed in our current study. Brown-Peterson et al. (2001) and van der Velde et al. (2010) reported that monthly GSI values corresponded with histological evidence of spawning times, supporting GSI as a proxy for the developmental state of ovaries. In our current study, the larger size range of oocytes, together with the higher GSI values, indicate that female cobia collected in South Carolina were closer to actually spawning than were specimens from previous studies.

Differences in the stage of cobia ovarian development between this and other studies may stem from locations where females were captured. In previous work, females were collected from coastal waters in the Gulf of Mexico (Lotz et al., 1996; Brown-Peterson et al., 2001) and off the Atlantic coast of the southeastern United States (Smith, 1996; Brown-Peterson et al., 2001). For the samples we examined, the mean GSI of females collected offshore (5.6) was closer to the means reported elsewhere (Biesiot et al., 1994; Lotz et al., 1996; Smith, 1996; Brown-Peterson et al., 2001). The dissimilarity of GSI values between female cobia collected inshore and those caught offshore was observed likely because those fish caught inshore were part of a spawning aggregation and those fish caught offshore were caught before or after spawning or were intercepted as they were migrating to spawning grounds. This hypothesis is supported

Table 4

The number of cobia (*Rachycentron canadum*) eggs (early-stage and late-stage) and larvae identified from plankton collections made in Port Royal Sound (PRS) and St. Helena Sound (SHS), South Carolina, in May and June 2008. Station codes: PA=PRS anchored net; SA=SHS anchored net; numbers correspond to a specific station. Station numbers with an asterisk were subsampled: numbers of eggs and larvae are estimated from the fraction sorted. No.=number of eggs or larvae; C=concentration (number/100 m^3).

		Early-stage eggs		Late-stage eggs		Larvae	
Date	Station	No.	C	No.	C	No.	C
6-May	PA-5			3	0.61		
8-May	SA-3	1	0.14				
14-May	PA-8					3	1.66
	PA-9					1	0.55
21-May	SA-1*	6	0.93	88	13.58	4	0.62
	SA-2			12	4.6		
	SA-3	2	0.28	9	1.27		
	SA-6*	4	0.56	12	1.69		
28-May	SA-1	2	0.38	16	3.08	1	0.19
	SA-3			13	2.64	5	1.01
29-May	PA-7			10	2.95	1	0.3
	PA-8			15	3.22		
	PA-9			3	0.64		
	PA-10			1	0.17	1	0.17
3-Jun	SA-1*	24	2.08	12	1.04	4	0.35
	SA-2*			56	7.06		
	SA-3*	496	62.51	64	8.07	4	0.5
	SA-6*			16	2.02		
	SA-7*			4	0.93	4	0.93
5-Jun	PA-7			4	0.57		
	PA-8	27	3.18	3	0.35	2	0.24
12-Jun	PA-7			15	4.26		
	PA-8			5	1.42	2	0.57
	PA-9					7	1.99
	PA10					1	0.19
18-Jun	SA-3			3	0.54	2	0.36

by recent genetic evidence that indicates the presence of distinct population segments along the southeastern coast of the United States (Darden[6]). In a study of the genetic structure of cobia caught offshore from Florida to Virginia and from inshore locations in South Carolina and Virginia, Darden found that fish collected offshore were a single population segment. Furthermore, the fish collected in inshore waters were genetically distinct from the offshore group and from cobia in other estuaries. If there is a distinct inshore South Carolina population segment, it could be maintained through spawning of cobia in their natal estuaries.

The distribution of female cobia among the reproductive phases may not represent the actual distribution in the population because the primary means of specimen collection was fishery dependent. In particular, the low percentages of females with developing and regressing ovaries and those females with histological signs of a recent spawn (POFs) are likely a result of fishery practices, particularly the seasonality of the recreational fishery. Cobia generally are thought to enter inshore waters when water temperatures reach 20°C (Richards, 1967; Smith, 1996), and water temperatures in PRS and SHS reached 20°C before the end of April in 2008. Recreational anglers, in contrast, targeted cobia most heavily in May (Steele[4]). Similarly, the fishing season for cobia may end before the fish leave inshore waters: the final plankton collections in PRS and SHS in mid-June contained cobia eggs and larvae, respectively, indicating spawning was still occurring in these areas despite a decrease in availability of specimens from recreational anglers. Female cobia with ovaries containing POFs were underrep-

[6] Darden, T. L. 2009. Personal commun. South Carolina Dept. Natural Resources, Charleston, SC 29412.

resented likely because of the time of day anglers were targeting fish. Evidence from both the histological analysis and plankton collections of eggs in this study suggests that wild cobia in South Carolina inshore waters spawn from mid-afternoon to late evening, with most activity occurring between 1530 and 1800 hr. Unfortunately, fish collected at tournaments were probably caught from morning to mid-afternoon, before the peak in daily spawning activity.

The best evidence produced from histological analysis that cobia were spawning inshore in South Carolina was the collection of actively spawning females. The duration of FOM is unknown for cobia, although this hormonally controlled "point-of-no-return" on the path to spawning commences 6 to 13 hr before spawning in spotted seatrout (Brown-Peterson et al., 1988; Roumillat and Brouwer, 2004), a co-estuarine inhabitant with cobia in the southeastern United States that spawns the same time of year. Because the earliest stages of FOM were unavailable to us, we were unable to estimate the time of FOM onset in cobia. However, both of the actively spawning females that we collected had oocytes that were in the late stages of FOM (near the mid-point of hydration), indicating that they would have spawned in the mid-afternoon and likely in the proximity of their capture.

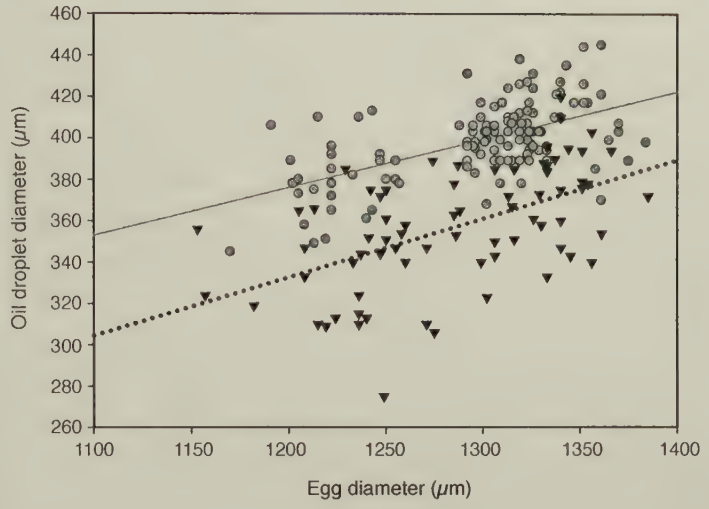

Figure 6

Regression lines for egg (ED) and oil-droplet (OD) diameters from preserved hatchery-reared cobia (*Rachycentron canadum*) eggs from the egg-development studies in 2007 and 2008 (circles, solid line; $y=0.23x+98.46$) and eggs identified as cobia from plankton collections conducted in Port Royal Sound and St. Helena Sound, South Carolina, in 2008 (triangles, dotted line; $y=0.28x-7.63$). Results of the analysis of covariance show no significant difference between the relationship of ED and OD of known cobia and suspected cobia eggs ($P=0.35$; overall coefficient of determination [r^2] $=0.61$).

Female cobia undergoing hydration have been collected in few studies, although there have been exceptions (Smith, 1996; van der Velde et al., 2010). Actively spawning females may compose a larger percentage of the inshore cobia population in South Carolina than the percentage reported here, but prespawners may not take a baited hook. As oocytes hydrate during FOM, their volume can nearly quadruple (Wallace and Selman, 1981). The ovaries of an actively spawning female caught in PRS composed one-sixth of the total body weight of the fish, nearly filling its entire body cavity. It is possible that cobia cease feeding during egg hydration.

Collection of cobia eggs in PRS and SHS also supports the idea that these areas are inshore spawning sites. Morphological features of wild cobia eggs matched closely those of hatchery-reared cobia eggs and were supported with the quantitative comparison of egg characteristics. Cobia eggs found in plankton collections had oil-droplet diameters within the reported range but smaller than the diameters reported for the hatchery-reared eggs. The hatchery eggs came from the spawns of only 2 females that had been hormonally induced to spawn, and maternal condition is known to affect egg and larval quality in fishes, including the size of oil droplets (Berkeley et al., 2004; Gagliano and McCormick, 2007; Sogard et al., 2008). Eggs collected in the plankton samples likely came from several females that encountered a variety of environmental conditions and had variable physiological conditions compared with the eggs from females reared in a controlled environment with a regular, strictly controlled diet.

The collection of eggs and larvae within PRS and SHS alone, although highly indicative of spawning, does not alone positively confer evidence of spawning habitat. Origin of late-stage larvae often cannot be determined: active dispersal or transport may be possible because of their increased swimming ability (Clark et al., 2005) or ability to control their vertical position in the water column, which allows migration by selective tidal stream transport (Boehlert and Mundy, 1988; Hogan and Mora, 2005). Cobia eggs were found in PRS from 12 to 20.5 km inshore. On the basis of the measured current speeds, a floating object could have traveled 7–15 km during a single flood tide, making it improbable that all eggs were spawned beyond the estuary. The most conclusive evidence for spawning within PRS comes from eggs that were estimated to be only 2–3 hr old and collected in the Broad River, 15.0 km inshore. With an average current speed of 0.7 m/s measured during the time of their collection, these eggs must have come from this estuary. In SHS, one particular collection of 496 early-stage eggs 9.7 km inshore lends compelling evidence that spawning occurred near the time and in the immediate vicinity of collection.

Table 5

Estimated age and time that cobia (*Rachycentron canadum*) eggs from plankton collections were spawned in Port Royal Sound (PRS) and St. Helena Sound (SHS), South Carolina, in 2008. Estimated spawning time is rounded down to the nearest quarter hour. Station codes: PA=PRS anchored net; SA=SHS anchored net; numbers correspond to a specific station.

		Sample pick-up		Estimated time of spawning	
Station	Date	Time	Age of eggs (hr)	Date	Time
SA01	5/21/2008	1816	19.5	5/20/2008	2045
SA02	5/21/2008	1835	21.5	5/20/2008	2100
SA03	5/21/2008	1850	21.5	5/20/2008	2115
SA06	5/21/2008	1920	21.5	5/20/2008	2145
SA01	5/28/2008	1237	19.5	5/27/2008	1700
SA03	5/28/2009	1304	19.5	5/27/2008	1730
PA07	5/29/2008	1350	21.5	5/28/2008	1615
PA08	5/29/2008	1405	21.5	5/28/2008	1630
PA09	5/29/2008	1425	21.5	5/28/2008	1700
SA01	6/3/2008	1827	25.5	6/2/2008	1700
SA02	6/3/2008	1850	25.5	6/2/2008	1720
SA03	6/3/2008	1900	25.5	6/2/2008	1730
SA06	6/3/2008	1923	25.5	6/2/2008	1800
PA07	6/5/2008	1912	26.0	6/4/2008	1715
PA08	6/5/2008	1927	2–3	6/5/2008	1630–1730
		1927	26.0	6/4/2008	1730
PA07	6/12/2008	1255	20.0	6/11/2008	1700
PA08	6/12/2008	1303	21.5	6/11/2008	1530
SA03	6/18/2008	1757	24.0	6/17/2008	1800

Conclusions

On the basis of the evidence provided here, cobia spawn in PRS and SHS during May and June. The collection of cobia eggs in early stages of development, the high average inshore GSI values, and the presence of actively spawning females in PRS and SHS makes this study the first one to positively document spawning of cobia in inshore waters. Spawning occurs in the afternoon and evening (primarily between 1530 and 1800 hr), as indicated by the embryological development of eggs and aging of wild-caught eggs. Some studies have suggested daytime and evening spawning of cobia based on the reported observation of what was believed to be spawning activity of adult cobia (see Shaffer and Nakamura, 1989), developmental stage of wild caught cobia eggs (Ditty and Shaw, 1992), and volitional spawning of a single female cobia held in captivity (Weirich et al., 2006); however, we documented daytime and evening spawning through multiple methods.

Intense recreational fishing can produce changes in fish populations and communities in ways similar to the effects of commercial fishing (Coleman et al., 2004; Cooke and Cowx, 2006). Moreover, hyperstability may mask overfishing conditions (Sadovy and Domeier, 2005), whereby catches remain constant at spawning aggregations as stocks decline, as observed in species such as the orange roughy (*Hoplostethus atlanticus)* (Clark et al., 2000; Koslow et al., 2000) and Nassau grouper (*Epinephelus striatus*) (Sala et al., 2001). Cobia found on the Atlantic coast of the United States were considered to be overfished by the SAFMC and GMFMC[3] in 1983, although the only assessment of the cobia fishery was conducted in the Gulf of Mexico (Williams, 2001). Since 1983, cobia has gained popularity among recreational anglers, as evidenced by the continual increase in effort by South Carolina charter boats since 1997 (Steele[4]).

Additional research needs to be conducted to determine the contribution of fish that spawn inshore to the overall U.S. Atlantic population of cobia because spawning may occur offshore as well, as hypothesized in other studies (Hassler and Rainville, 1975; Smith, 1996; Burns et al.[1]). Documentation of spawning in PRS and SHS indicates that inshore waters elsewhere in their region may also provide critical habitat for cobia. Together, the documented spawning and the discovery of a unique population segment within South Carolina inshore waters (Darden[4]) provide compelling reasons for management agencies to reconsider current management strategies. To treat all cobia in U.S. waters as a single population may no longer be appropriate, and the possible existence of regional, self-sustaining population segments should be taken into account.

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Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity

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Abstract—Most assessments of fish stocks use some measure of the reproductive potential of a population, such as spawning biomass. However, the correlation between spawning biomass and reproductive potential is not always strong, and it likely is weakest in the tropics and subtropics, where species tend to exhibit indeterminate fecundity and release eggs in batches over a protracted spawning season. In such cases, computing annual reproductive output requires estimates of batch fecundity and the annual number of batches—the latter subject to spawning frequency and duration of spawning season. Batch fecundity is commonly measured by age (or size), but these other variables are not. Without the relevant data, the annual number of batches is assumed to be invariant across age. We reviewed the literature and found that this default assumption lacks empirical support because both spawning duration and spawning frequency generally increase with age or size. We demonstrate effects of this assumption on measures of reproductive value and spawning potential ratio, a metric commonly used to gauge stock status. Model applications showed substantial sensitivity to age dependence in the annual number of batches. If the annual number of batches increases with age but is incorrectly assumed to be constant, stock assessment models would tend to overestimate the biological reference points used for setting harvest rates. This study underscores the need to better understand the age- or size-dependent contrast in the annual number of batches, and we conclude that, for species without evidence to support invariance, the default assumption should be replaced with one that accounts for age- or size-dependence.

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The relationship between reproductive output and subsequent recruitment of new individuals is fundamental to population dynamics. In stock assessments, this relationship is typically quantified by using a spawner–recruit model. Such models were originally developed with population fecundity as the measure of spawners, but most current applications use spawning biomass, calculated as the total weight of mature females (Rothschild and Fogarty, 1989). A critical assumption with this approach is that spawning biomass accurately represents the reproductive potential of a stock. However, this assumption does not always hold (Trippel, 1999; Marshall et al., 2003, 2006) and, when violated, can inject error into assessment models and subsequent management advice (Rothschild and Fogarty, 1989; Murawski et al., 2001; Scott et al., 2006). Thus, recognition is growing for the need to integrate more reproductive biology into stock assessments by replacing spawning biomass with more accurate measures of reproductive potential (Trippel, 1999; Morgan, 2008; Witthames and Marshall, 2008).

Much of the work to date on reproductive potential and stock assessments comes from investigations on gadoids, pleuronectids, and other high-latitude species that typically have determinate fecundity patterns (Trippel, 1999; Murawski et al., 2001; Morgan, 2008; Witthames and Marshall, 2008; Morgan et al., 2009). Fewer studies have been conducted on fish species with indeterminate fecundity, in part because the data requirements can be more daunting (Lowerre-Barbieri et al., 2011a, 2011b). Many warm-water marine species from the subtropics (latitudes <40°) spawn multiple batches per year, usually over a protracted spawning season. For example, species off the southeastern United States typically spawn several times within a 3–4 month duration (Cuellar et al., 1996; McGovern et al., 1998; Waggy et al., 2006). Near the tropics, spawning seasons are even longer and often associated with peak (but variable) activity when local conditions favor transport and survival of offspring (Johannes, 1978; Thresher, 1984). Such extended patterns of

spawning, or extended readiness to spawn, are typical of indeterminate spawners with asynchronous oocyte development patterns (Hunter et al., 1985; Murua et al., 2003). Although many species that exhibit determinate fecundity also spawn in batches, quantifying annual fecundity for indeterminate spawners requires estimates of batch fecundity (i.e., eggs per batch) and number of batches per year, each as a function of parental age or size (Murua et al., 2003). Estimating the number of batches per year requires knowledge about spawning season duration and spawning frequency within the season (or average time between batches), including any temporal patterns of that frequency (Murua et al., 2003). Then, annual fecundity of indeterminate species can be calculated as the product of the number of eggs per batch and the number of batches per year.

Estimation of batch fecundity by age is relatively straightforward (Porch et al., 2007). In fact, these estimates tend to relate linearly to body weight, and this relationship has been the rationale for the use of spawning biomass as a proxy for total egg production. However, estimation of spawning season duration and spawning frequency by size or age is much more difficult. Despite recognition from individual studies that frequency and duration of spawning may increase with age and size (Lowere-Barbieri et al., 2011a), much of this information is lacking for many species. Without information, the typical default assumption in stock assessment is that both spawning duration and frequency are invariant across age. Widespread application of this assumption of invariance raises 2 key questions. Is the assumption justified? If not, what are the consequences for stock assessment and resulting management advice? We address the first question through a review of the literature and the second one by modeling effects of age-dependent spawning activity (annual number of batches) on spawning potential ratio (Goodyear, 1993; Shertzer et al., 2008) and reproductive value (both of these metrics are defined in the next section).

Materials and methods

Review of scientific literature—spawning frequency and duration

To examine whether or not age and size effects on spawning duration and frequency were common, we reviewed scientific literature on fishes, including aquaculture studies that investigated natural spawning (nonhormonally induced), as well as field studies. Although most of these studies were of marine species, freshwater species were not excluded from this review. In addition, our search included species not necessarily classified as indeterminate spawners because relatively few studies distinguish fecundity pattern (Murua et al., 2003). Our review proceeded in 2 stages. First, we selected articles in which batch spawning frequency was examined, either as spawning fraction (proportion of mature fish actively spawning), number of batches within a fixed time period, or average time interval between batches. From these articles, we further narrowed the list to those that reported the relationship (or lack thereof) between spawning frequency and age or size. Second, we selected articles in which spawning duration was examined by age or size. Numerous articles reported the season or duration of spawning, but duration by age or size was examined in relatively few of them. Thus, in this second review, we did not restrict our search to batch spawners; instead, we noted any study that reported spawning duration by age or size.

Implications for stock assessment and management

To examine how the age-dependent annual number of batches affects stock assessment results and management advice, we used classical per-recruit analyses (Shertzer et al., 2008) of spawning potential ratio and reproductive value. Standard fishery equations described equilibrium abundance of females at age (N_a), weight at age (W_a), maturity at age (m_a), fecundity at age of mature fish (f_a), and selectivity of fishing gear (s_a) (Table 1). These analyses are "per recruit" by virtue of scaling to an initial abundance of one (N_1=1). To populate our model with parameter values representing warm-water marine fishes, we used average life-history characteristics reported for the Gulf of Mexico (Table 2). Fishes of this region tend to be characterized by indeterminate fecundity and batch spawning, in contrast to fishes from higher latitudes where determinate fecundity is more common.

Annual fecundity at age was determined as the product of eggs produced per batch (assumed to be proportional to body weight) and the annual number of batches, which implicitly accounted for joint effects of spawning frequency and spawning duration. The annual number of batches at age followed 1 of 4 qualitative patterns: constant, increasing, decreasing, or dome shaped (Fig. 1A). To create these patterns, we first set the constant pattern to a value of 1, and then we scaled the remaining patterns such that the 4 patterns had equal integration (i.e., area under the curve). Although not all these patterns were prevalent in the literature review, we included all for completeness and comparison. In this article, we report spawning potential ratio and reproductive value across these 4 patterns.

Spawning potential ratio Spawning potential ratio (Goodyear, 1993; Shertzer et al., 2008) was computed by using standard fishery equations (Table 1):

$$\Psi_F = \phi_F / \phi_0 . \quad (1)$$

The numerator (ϕ_F) of this ratio quantified expected reproductive output (e.g., fecundity) per recruit under fishing rate F,

$$\phi_F = \sum_{a=1}^{A_{max}} f_a m_a N_a , \quad (2)$$

Table 1

Model equations used in our per-recruit analysis of spawning potential ratio and reproductive value.

Equation	Description
$N_1 = 1$ $N_{a+1} = N_a e^{-(s_a F + M)}$	Equilibrium number of females (N_a) per recruit at age a—a function of selectivity at age (s_a), fishing mortality rate (F), and natural mortality rate (M)
$s_a = \frac{1}{1+e^{-(\rho_s(a-A_s))}}$	Selectivity at age—a logistic function characterized by a slope parameter (ρ_s) and age of 50% selectivity (A_s)
$m_a = \frac{1}{1+e^{-(\rho_m(a-A_m))}}$	Maturity at age (m_a)—a logistic function characterized by a slope parameter (ρ_m) and age of 50% maturity (A_m)
$W_a = \left[L_\infty\left(1-e^{-Ka}\right)\right]^\tau$	Weight at age (W_a)(von Bertalanffy, 1938)—a function of asymptotic length (L_∞), somatic growth parameter (K), and an exponent (τ) relating length to weight
$b_a^i = c_i\left(\frac{1}{1+e^{-\left(\rho_1(a-A_b)+\rho_2(a-A_b)^2\right)}}\right)$	Annual number of batches spawned at age (b_a) per mature female—a function of 3 parameters (ρ_1, ρ_2, A_b), scaled by a constant c_i so that the area under the curve is the same for each spawning pattern i (Fig. 1)
$f_a^i = b_a^i W_a$	Annual fecundity at age (f_a) per mature female of spawning pattern i. Batch fecundity was assumed to be proportional to body weight

Table 2

Model parameters used in the per-recruit analysis of spawning potential ratio and reproductive value. Means of values reported for Gulf of Mexico reef fishes are taken from Table 1 of Farmer et al.[1], excluding sand perch (*Diplectrum formosum*) because of an apparent error and deepwater tilefishes and groupers because they inhabit waters typically colder than the waters of tropical and subtropical species.

Parameter	Value	Description	Source
A_{max}	22	Maximum age; ages modeled are 1, 2,..., A_{max}	Farmer et al.[1]
M	$M = 4.22/A_{max} = 0.19$	Natural mortality rate	Hewitt and Hoenig, 2005
F	Range [0.0, 0.6]	Fishing mortality rate	Independent variable
L_∞	1.0	Asymptotic length	Assumed
K	0.19	Somatic growth parameter	Farmer et al.[1]
τ	3.0	Exponent relating body length to weight	Assumed
A_m	3.16	Age of 50% maturity	Farmer et al.[1]
A_s	$A_S = A_{max}/4 = 5.5$	Age of 50% selectivity	Assumed
ρ_m, ρ_s	1.0	Slope of logistic maturity or selectivity, respectively	Assumed
ρ_1, ρ_2, A_b for $i = 1$	∞, ∞, 0.0	Spawning frequency constant with age	Control variables
ρ_1, ρ_2, A_b for $i = 2$	0.5, 0.0, $A_{max}/2$	Spawning frequency increases with age	Control variables
ρ_1, ρ_2, A_b for $i = 3$	−0.5, 0.0, $A_{max}/2$	Spawning frequency decreases with age	Control variables
ρ_1, ρ_2, A_b for $i = 4$	0.5, −0.05, $A_{max}/4$	Spawning frequency dome-shaped with age	Control variables

[1] Farmer, N. A., R. P. Malinowski, and M. F. McGovern. 2010. Species groupings for management of the Gulf of Mexico reef fish fishery. NOAA, NMFS, SERO-LAPP-2010-03 Rep., 32 p.

where f_a = annual fecundity at age a (the product of batch fecundity and number of batches per year);
m_a = maturity at age; and
N_a = relative abundance at age, discounted through time by natural mortality and fishing rates (Table 1).

The denominator (ϕ_0) of this ratio was similarly computed, but with N_a discounted only by natural mortality. Thus, Ψ_F measured effects of fishing on the expected reproductive output per recruit relative to the output under no fishing. It decreased with increased fishing rate.

Spawning potential ratio was suggested conceptually by Goodyear (1977), and its use remains widely

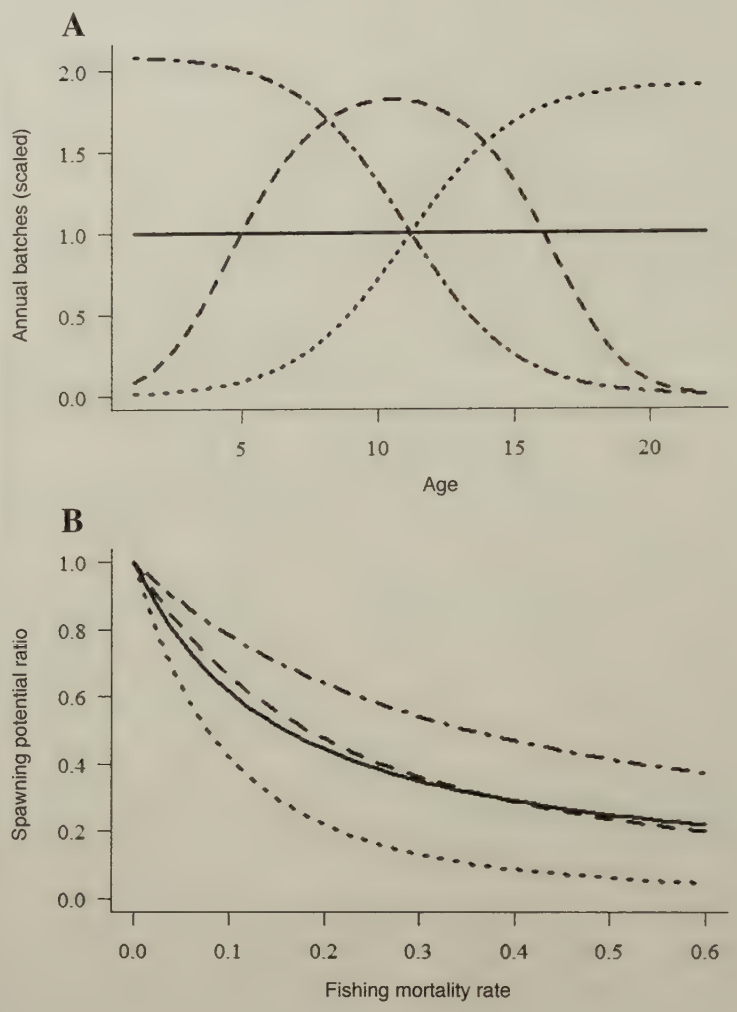

Figure 1

(**A**) Annual number of batches spawned per mature female, based on 4 qualitative patterns used in our per-recruit analysis of spawning potential and reproductive value: constant (i=1, solid line), increasing (i=2, dotted line), decreasing (i=3, dash-dot line), and dome-shaped (i=4, dashed line). (**B**) Spawning potential ratio as a function of fishing mortality rate. Model equations and parameters are given in Tables 1 and 2 respectively.

popular in stock assessments for 2 reasons. First, data requirements are low relative to other age-structured assessment approaches; for example, computation does not depend on a spawner–recruit relationship. Second, the spawning potential ratio can provide biological reference points for fishery management (Caddy and Mahon, 1995), in particular for a target fishing rate $F_{X\%}$. The fishing rate $F_{X\%}$ is defined as the F that provides $X\%$ of reproductive output per recruit relative to the unfished output level (i.e., spawning potential ratio expressed as a percentage). In many cases, $F_{X\%}$ is used as a proxy for the F associated with maximum sustainable yield (F_{MSY}). Mace (1994) suggested a default proxy of $F_{40\%}$ when the spawner–recruit relationship is unknown; however, the appropriate level of $X\%$ will depend on life-history and fishery characteristics (Clark, 2002; Williams and Shertzer, 2003; Brooks et al., 2009).

Reproductive value Reproductive value (V_a) measures the age-dependent contribution to population growth by combining survivorship and fecundity, the 2 life-history elements crucial to fitness. The concept of reproductive value has been applied most commonly to examine life-history evolution (Goodman, 1982; Stearns, 1992), but it also has been suggested as useful in the context of fishery management (MacArthur, 1960; Ware, 1985; Xu et al., 2012). For example, MacArthur (1960) argued that

the highest harvest rates can be achieved by removing first those ages with the lowest reproductive value. For our purposes, we use reproductive value to demonstrate the importance of older fish toward population growth and to quantify how that importance depends on the pattern of annual number of batches.

We computed reproductive value of a stationary population as the expected number of offspring produced by an individual from age a until the end of the lifespan (A_{max}):

$$V_a = \sum_{x=a}^{A_{max}} \frac{l_x}{l_a} g_x, \quad (3)$$

where l_x = the probability that an individual survives to age x; and
g_x = the mean number of offspring produced by an individual of age x (Stearns, 1992), here the product of annual fecundity and maturity.

Because this analysis was conducted on a per-recruit basis, l_x was equivalent to N_a of Table 1. The term l_x/l_a was the probability of surviving to age x conditional on having survived to age a. To examine implications for optimal management strategies, we computed V_a across a range of fishing rates. For each of the 4 qualitative patterns in annual spawning frequency, we report V_a in the absence of fishing in addition to the age for which V_a was maximized as a function of fishing rate.

Results

Review of the literature—spawning frequency and duration

In our review of spawning frequency, we found 208 articles that reported multiple batches and indicated some information about the frequency or number of batches occurring within a specified time period. Only 20% (41 articles, 34 species) presented findings about spawning frequency related to age or size (Table 3). Of this subset, most (28 articles, 21 species) reported increases of spawning frequency with age or size. Some (9 articles, 9 species) reported no effect, but several of these articles cautioned about lack of power. Only 4 articles (4 species) indicated a decrease in spawning frequency with age or size.

We found that if we tried to restrict our review of spawning frequency to stocks or species that exhibit indeterminate fecundity, we would have had a challenging task. Of the articles (n=208) reporting some information about spawning frequency, only 52 were explicit about fecundity type or oocyte development pattern, and most (38) of them indicated an indeterminate type. Of the 41 articles reporting a spawning frequency trend by size or age, 10 indicated a fecundity type and 7 reported an indeterminate type.

In our review of spawning duration, we found 33 articles (28 species) that reported results related to age or size (Table 4). Of these articles, most (28 articles, 23 species) of them reported increased spawning duration with age or size. Several articles noted no change (5 articles, 5 species). None of them mentioned a decreased duration with age or size.

Implications for stock assessment and management

Across all levels of fishing, spawning potential ratio was highest when batch production decreased with age and lowest when it increased with age (Fig. 1B). Therefore, an incorrect assumption about annual batch production could lead to substantial bias in biological reference points and consequently in resulting management advice. For example, in this model, $F_{40\%}$ equals 0.24 for age-invariant batch production, $F_{40\%}$ equals 0.11 for increasing production, $F_{40\%}$ equals 0.53 for decreasing production, and $F_{40\%}$ equals 0.26 for dome-shaped production. If the actual pattern was that of increasing batch production but was incorrectly assumed to be age invariant, the estimated $F_{40\%}$ would be biased high by 118%.

As with spawning potential ratio, reproductive value was sensitive to the spawning pattern. In the absence of fishing, older females were considerably more important to population growth in cases of constant or increasing batch production than in cases of decreasing or dome-shaped batch production (Fig. 2A). For example, with the increasing pattern, reproductive value exceeded a value of 5 and was maximized near age 14, indicating that a fish of that age can produce more than 5 times the number of offspring throughout its remaining lifespan than can a fish of age 1. With the decreasing pattern, the maximum reproductive value was less than twice the value of fish at age 1 and occurred near age 6. As the rate of fishing increased, the age of maximum reproductive value shifted toward older fishes in each case but did so more quickly and to much older ages in cases of constant or increasing batch production (Fig. 2B). This result highlights the importance of older individuals for population growth.

Discussion

Our review of literature on batch spawning revealed that most studies have not examined, or at least have not reported, size- or age-dependent effects. In those studies where spawning frequency was examined, the majority of species (62%) were found to spawn more often with increasing age or size. Similarly, in those studies where spawning duration was examined, the majority of species (82%) were found to spawn over a longer duration with increasing age or size. These patterns of increasing spawning frequency and duration were common but not universal. Several studies found no discernible change with age or size, and patterns of decreases with age or size appeared to be rare. Although 1 of 2 articles on Atlantic cod (*Gadus morhua*) found spawning frequency to decrease with age (Kjesbu et al., 1996), that article

Table 3

Patterns of spawning frequency by age or size based on a review of spawning frequency within the scientific literature on fish reproduction.

Spawning frequency	Species	Reference(s)
Increases with size or age	*Atherina boyeri* (sand smelt, Atherinidae)	Tomasini et al., 1996
	Cynoscion nebulosus (spotted seatrout, Sciaenidae)	Crabtree and Adams[1]; Roumillat and Brouwer, 2004; Brown-Peterson, 2003; Lowerre-Barbieri et al., 2009
	Danio rerio (zebra danio, Cyprinidae)	Uusi-Heikkilä et al., 2010
	Engraulis mordax (northern anchovy, Engraulidae)	Parrish et al., 1986
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Claramunt et al., 2004, 2007
	Gasterosteus aculeatus (threespine stickleback, Gasterosteidae)	Wootton, 1973
	Hemiramphus brasiliensis (ballyhoo, Hemiramphidae)	McBride and Thurman, 2003
	Limanda aspera (yellowfin sole, Pleuronectidae)	Nichol and Acuna, 2001
	Lutjanus campechanus (red snapper, Lutjanidae)	Collins et al., 2001
	Melanogrammus aeglefinus (haddock, Gadidae)	Trippel and Neil, 2004
	Merluccius hubbsi (Argentine hake, Merlucciidae)	Macchi et al., 2004
	Mycteroperca microlepis (gag, Serranidae)	Collins et al., 1998
	Ocyurus chrysurus (yellowtail snapper, Lutjanidae)	Trejo-Martinez et al., 2011
	Sardinops ocellatus (southern African pilchard, Clupeidae)	LeClus, 1989
	Sardina pilchardus (true sardine, Clupeidae)	Perez et al.[2]; Garcia et al., 1992; Quintanilla and Perez, 2000; Ganias et al., 2003a
	Sciaenops ocellatus (red drum, Sciaenidae)	Roberts et al., 1978
	Scomber japonicus (Pacific chub mackerel, Scombridae)	Dickerson et al., 1992
	Solea solea (sole, Soleidae)	Witthames[3]
	Sprattus sprattus balticus (Baltic sprat, Clupeidae)	Kraus and Koster, 2004
	Tautoga onitis (tautog, Labridae)	LaPlante and Schultz, 2007
	Thunnus albacares (yellowfin tuna, Scombridae)	McPherson, 1991
Decreases with size or age	*Clupea bentincki* (Chilean herring, Clupeidae)	Cubillos et al., 2007
	Engraulis australis (Australian anchovy, Engraulidae)	Dimmlich et al., 2009
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Cubillos et al., 2007
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu et al., 1996
No change with size or age	*Decapterus punctatus* (round scad, Carangidae)	McBride et al., 2002
	Engraulis mordax (northern anchovy, Engraulidae)	Hunter and Macewicz, 1980
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu, 1989
	Hyphessobrycon pulchripinnis (lemon tetra, Characidae)	Burt et al., 1988
	Lepomis gibbosus (pumpkinseed, Centrarchidae)	Fox and Crivelli, 1998
	Pogonias cromis (black drum, Sciaenidae)	Nieland and Wilson, 1993
	Seriphus politus (queenfish, Sciaenidae)	DeMartini and Fountain, 1981
	Stegastes partitus (bicolor damselfish, Pomacentridae)	Cole and Sadovy, 1995
	Tilapia zillii (redbelly tilapia, Cichlidae)	Coward and Bromage, 1999

[1] Crabtree, R. E., and D. H. Adams. 1998. Spawning and fecundity of spotted seatrout, *Cynoscion nebulosus*, in the Indian River Lagoon, Florida. *In* Investigations into nearshore and estuarine gamefish abundance, ecology, and life history in Florida, p. 526–566. Technical Report for Federal Aid in Sportfish Restoration Act Project F-59. Florida Dept. Environmental Protection, Florida Mar. Res. Inst., St. Petersburg, FL.

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Table 4

Patterns of spawning duration by age or size based on a review of spawning season duration within the scientific literature on fish reproduction.

Spawning Duration	Species	Reference(s)
Increases with size or age	*Atherina boyeri* (sand smelt, Atherinidae)	Tomasini et al., 1996; Tomasini and Laugier, 2002
	Clupea bentincki (Chilean herring, Clupeidae)	Cubillos and Claramunt, 2009
	Cynoscion nebulosus (spotted seatrout, Sciaenidae)	Lowerre-Barbieri et al., 2009
	Engraulis encrasicolus (European anchovy, Engraulidae)	Millan, 1999
	Engraulis mordax (northern anchovy, Engraulidae)	Parrish et al., 1986
	Engraulis ringens (Peruvian anchoveta, Engraulidae)	Claramunt et al., 2007; Cubillos and Claramunt, 2009
	Gadus morhua (Atlantic cod, Gadidae)	Kjesbu et al., 1996; Lawson and Rose, 2000
	Genyonemus lineatus (white croaker, Sciaenidae)	Love et al., 1984
	Hemiramphus brasiliensis (ballyhoo, Hemiramphidae)	McBride and Thurman, 2003
	Lepomis gibbosus (pumpkinseed, Centrarchidae)	Fox and Crivelli, 1998
	Leuresthes tenuis (California grunion, Atherinidae)	Clark, 1925
	Lutjanus carponotatus (stripey sea perch, Lutjanidae)	Kritzer, 2004
	Melanogrammus aeglefinus (haddock, Gadidae)	Trippel and Neil, 2004
	Merluccius hubbsi (Argentine hake, Merlucciidae)	Macchi et al., 2004
	Sardina caerulea (Californinia sardine, Clupeidae)	Clark, 1934
	Sardina pilchardus (true sardine, Clupeidae)	Zwolinski et al., 2001
	Sardina pilchardus sardina (Mediterranean sardine, Clupeidae)	Ganias et al., 2003b
	Sardinops ocellatus (southern African pilchard, Clupeidae)	LeClus, 1989
	Sardinops sagax (Pacific sardine, Clupeidae)	Claramunt and Herrera, 1994
	Scomber japonicus (Pacific chub mackerel, Scombridae)	Dickerson et al., 1992; Knaggs and Parrish[1]; MacCall et al., 1980
	Seriphus politus (queenfish, Sciaenidae)	DeMartini and Fountain, 1981
	Solea solea (sole, Soleidae)	Witthames[2]
	Trachurus symmetricus (jack mackerel, Carangidae)	Wine and Knaggs[3]
No change noted overall, but larger fish develop eggs and/or spawn earlier	*Clupea harengus* (Atlantic herring, Clupeidae	Lambert, 1987
	Clupea pallasi (Pacific herring, Clupeidae)	Ware and Tanasichuk, 1989
	Cynoscion regalis (weakfish, Sciaenidae)	Lowerre-Barbieri et al., 1996
	Scomber scombrus (Atlantic mackerel, Scombridae)	Priede and Watson, 1993
	Trachurus trachurus (horse mackerel, Carangidae)	Abaunza et al., 2003

[1] Knaggs, E. H., and R. H. Parrish. 1973. Maturation and growth of Pacific mackerel *Scomber japonicus* Houttuyn. Marine Resources Tech. Rept. 3, 19 p. Calif. Dept. Fish and Game, Long Beach, CA.

[2] Witthames, P. R. 2003. Methods to assess maturity and realized fecundity illustrated by studies on Dover sole *Solea solea*. *In* Report of the working group of modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids; 4–7 September 2001, Bergen, Norway (O. S. Kjesbu, J. R. Hunter and P. R. Witthames, eds.), Fisken og havet. no. 12-2003, p. 125–138. Inst. Mar Res., Bergen, Norway.

[3] Wine, V. L., and E. H. Knaggs. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Mar. Resources Tech. Rept 32, p. 1–25. Calif. Dept. Fish and Game, Long Beach, CA,

also found that older fish had greater annual fecundity, and less frequent spawning over a longer season. In other cases, mediating factors, such as temperature or productivity, may have explained an anomalous size-based trend. Two articles on anchovies and a sardine reported lower spawning frequency among larger-size fish of stocks in shelf waters that were geographically separated from smaller fish in warmer coastal waters (Cubillos et al., 2007; Dimlich et al., 2009). Elsewhere, one of the anchovy species, Peruvian anchoveta (*Engraulis ringens*), was noted to have a positive relationship of size with both spawning frequency (Claramunt et al., 2004, 2007) and duration (Claramunt et al., 2007; Cubillos and Claramunt, 2009). From life-history theory, we would expect older fishes to invest relatively more energy into reproduction (Stearns, 1992); however, increased investment could manifest in various ways (e.g., egg quality rather than quantity; Berkeley et al., 2004a, 2004b). Empirical observations, as reviewed here, were necessary to elucidate patterns in the annual number of batches. The common assumption of age or size invariance would appear to be generally wrong.

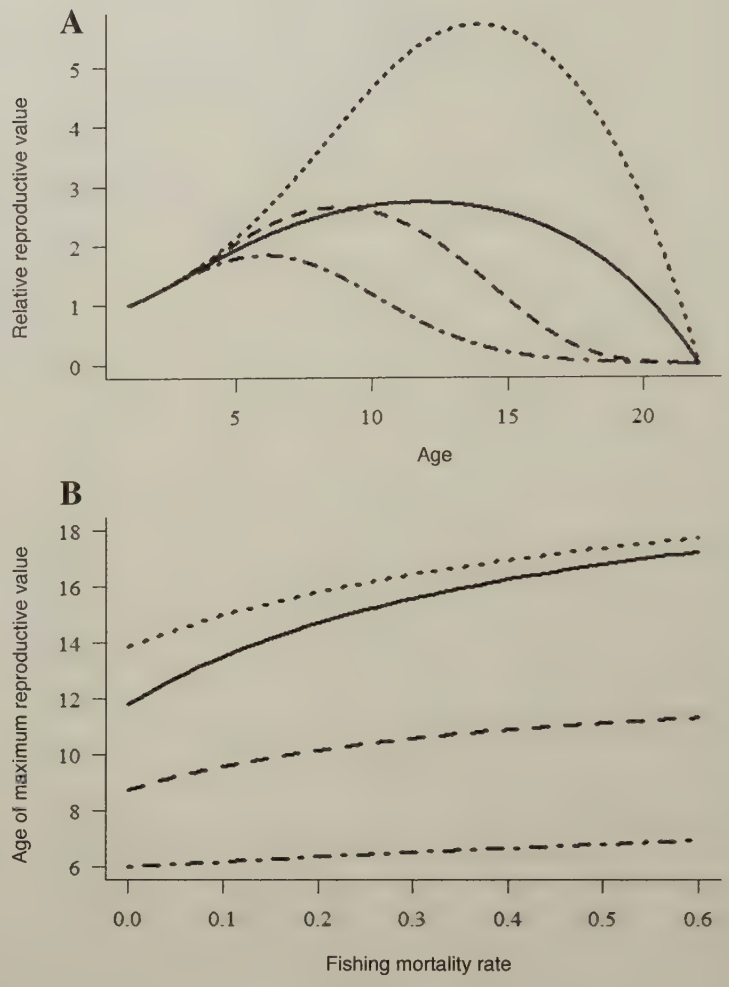

Figure 2

(**A**) Reproductive value incorporating survival, maturity, batch fecundity, and 4 qualitative patterns of annual number of batches. Results are based upon these qualitative patterns are shown in relation to the value at age 1, computed as a function of age under natural mortality only. (**B**) Age of maximum reproductive value as a function of fishing-induced mortality rate. In both panels, annual number of batches spawned (shown in Fig. 1A) per mature female are constant (i=1, solid line), increasing (i=2, dotted line), decreasing (i=3, dash-dot line), and dome-shaped (i=4, dashed line).

Measures of mean spawning frequency and duration are commonly applied to derive estimates of spawning stock biomass through the daily egg production method (DEPM) in species with indeterminate fecundity (Stratoudakis et al., 2006). Although this method is difficult to apply with precision, the DEPM has been used most often in assessments of short-lived clupeoid species for which direct methods of estimating spawning biomass are preferred (Stratoudakis et al., 2006). Because this approach is not explicitly dependent on age structure, the implications of size and age variation should be minimal. However, Priede and Watson (1993) provide an example of the difficulties in applying the DEPM to a longer-lived species, including the case when older Atlantic mackerel (*Scomber scombrus*) begin spawning earlier than younger mature females. The knowledge that older adults may spawn earlier, over a longer season, or more often to produce more batches may help guide sampling designs. Sampling of adults should be representative of a population or enough information on stock structure should be gathered to properly weight the adult data used for DEPM (Stratoudakis et al., 2006).

In contrast to application of egg production methods to short-lived species, our results may be most informative for estimates of reproductive potential used in age-structured assessments of relatively long-lived species

that have been shown or must be assumed to be indeterminate spawners. When information is lacking to make a distinction about fecundity type, the recommendation is to follow an indeterminate approach that, in theory, will give accurate estimates of annual fecundity regardless of fecundity type (Lowerre-Barbieri et al., 2011b).

Applications of our model showed substantial sensitivity to age dependence in the annual number of batches. If the annual number of batches increased with age but was incorrectly assumed constant, stock assessment models tended to overestimate the biological reference points used for setting harvest rates. We found this result to be true for rates based on spawning potential ratio (Fig. 1B), as well as for those rates based on maximum sustainable yield.

This source of error in the determination of harvest rate may be of particular concern when management is based on output controls, such as annual catch limits, where the estimation of absolute scale of a population matters. However, it is not straightforward to predict a priori the consequences of all the interactions within an assessment model. For example, age dependence of spawning may not affect the estimated number of recruits (Morgan et al., 2007) but could affect the estimated spawning biomass and, therefore, the estimated spawner–recruit curve. As a result, the erroneous assumption of age invariance may be a common source of the error-in-variables problem identified in spawner–recruit estimation (Walters and Ludwig, 1981). Whether through error-in-variables or other latent assumptions, inadequately accounting for the effects of age structure on reproductive potential can result in poor prediction of stock status (Witthames and Marshall, 2008; Murua et al., 2010).

Our study adds to a growing list of age-dependent characteristics shown to influence reproductive success, including skipped spawning (Jørgensen et al., 2006; Secor, 2008; Rideout and Tomkiewicz, 2011), egg or larval quality (O'Farrell and Botsford, 2006; Spencer et al., 2007), and senescence (Woodhead, 1979; Porch et al., 2007). The first 2 characteristics likely would (although not necessarily) increase the value of older fishes beyond that considered by our models, and senescence would likely decrease the value of older fishes for population growth. Another consideration more difficult to ascertain is the influence of males on reproductive success (Van Doornik et al., 2008). Although our models predicted recruitment through the conventional use of only females, some other assessments model stock productivity as a function of both sexes (Brooks et al., 2008). Sperm limitation may be important in population dynamics if sex ratio fluctuates with changes in population structure, as it does, for example, in hermaphroditic fishes, particularly if the sperm quality, production, or allocation depends on age or size (Brooks et al., 2008; Uusi-Heikkilä et al., 2012).

In many assessments, spawning biomass is used in place of total egg production, either for simplicity or because no reliable information on batch fecundity exists. Because batch fecundity typically scales with body weight (Hunter et al., 1985; Porch et al., 2007; but see Dick, 2009), the use of spawning biomass may serve as a first-order approximation, particularly when no other measure of reproductive potential is available. To additionally account for increased number of batches, the age-based vector of body weight can be multiplied by an age-based vector ($\boldsymbol{b}$) of annual number of batches. In essence, this technique generalizes the usual approach, where $\boldsymbol{b}=\mathbf{1}$ is assumed. An increasing vector would seem more credible and, in data-limited cases, could be obtained by borrowing data from similar species or from meta-analysis.

Indeed, we initially considered a meta-analysis of the studies from our literature review. However, after examining the data as reported, we did not think we could provide meaningful, quantitative analyses. In aggregate, those studies were more useful in the qualitative sense of identifying patterns of increase, decrease, or no change in the number of batch spawnings. We anticipate that quantitative meta-analysis will become possible as more detailed data on batch spawning are collected. Lowerre-Barbieri et al. (2011a) provide guidance on the standardized information and approaches needed for estimating spawning frequency and duration.

We also desired to categorize the results of our literature review by fecundity type, but we could identify only a trend for indeterminate type among studies reporting multiple spawning. Most studies did not explicitly indicate either fecundity type or oocyte recruitment pattern. For warm-water species, indeterminate fecundity type is often assumed but not proven, and, as mentioned earlier, this assumption can be a robust one for estimating annual fecundity (Lowerre-Barbieri et al., 2011b). Careful review within the literature by species may yield more insight, but fecundity type often may defy easy categorization because the synchrony of oogenesis and resulting fecundity type may vary even within a species. Different stocks, especially those separated by latitudinal zones, may exhibit different fecundity types (Abaunza et al., 2003). Therefore, multiple criteria are recommended for defining fecundity type (Murua and Saborido-Rey, 2003; Lowerre-Barbieri et al., 2011b) and, accordingly, some corrections have been made to previous classifications (Arocha, 2002).

Conclusions

The 2 principal findings of this study are that, for fishes with indeterminate or uncertain fecundity type, age (size) dependence in the annual number of batches is more common than age invariance and that this dependence merits consideration in population models. For many species, stock assessments could be improved by collecting age-specific information on spawning frequency and duration. Without such information, or unless data indicate otherwise, the assumption that annual spawning increases with age may be more plausible than the currently common assumption of age invariance.

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Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary

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Abstract—The transition between freshwater and marine environments is associated with high mortality for juvenile anadromous salmonids, yet little is known about this critical period in many large rivers. To address this deficiency, we investigated the estuarine ecology of juvenile salmonids and their associated fish assemblage in open-water habitats of the lower Columbia River estuary during spring of 2007–10. For coho (*Oncorhynchus kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and yearling (age 1.0) Chinook (*O. tshawytscha*) salmon, and steelhead (*O. mykiss*), we observed a consistent seasonal pattern characterized by extremely low abundances in mid-April, maximum abundances in May, and near absence by late June. Subyearling (age 0.0) Chinook salmon were most abundant in late June. Although we observed interannual variation in the presence, abundance, and size of juvenile salmonids, no single year was exceptional across all species-and-age classes. We estimated that >90% of juvenile Chinook and coho salmon and steelhead were of hatchery origin, a rate higher than previously reported. In contrast to juvenile salmonids, the abundance and composition of the greater estuarine fish assemblage, of which juvenile salmon were minor members, were extremely variable and likely responding to dynamic physical conditions in the estuary. Comparisons with studies conducted 3 decades earlier suggest striking changes in the estuarine fish assemblage—changes that have unknown but potentially important consequences for juvenile salmon in the Columbia River estuary.

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The Columbia River was historically home to one of the largest Pacific salmon (*Oncorhynchus* spp.) runs in the world, with 10–16 million adult salmon and steelhead (hereafter collectively referred to as *salmon*) returning to the basin annually before European settlement (NRC, 2004). As human population and activities have increased over the last century (Sherwood et al., 1990; NRC, 1996), Columbia River salmon runs have declined to the point that adult returns are typically less than 10% of historical levels (PFMC, 2011). Furthermore, more than half of the salmon populations in the river basin are thought to have become extinct (Gustafson et al., 2007), and most extant wild populations receive protection under the U.S. Endangered Species Act (ESA) as threatened or endangered species (Ford, 2011). This protected species list includes 5 subgroups of steelhead ([*O. mykiss*]; lower, middle, and upper Columbia River and Snake and Willamette rivers) and 1 subgroup each of coho ([*O. kisutch*]; lower Columbia River), chum ([*O. keta*]; Columbia River), and sockeye ([*O. nerka*]; Snake River) salmon (Ford, 2011). Also listed are 5 subgroups of Chinook salmon (*O. tshawytscha*): lower Columbia River, Snake River spring and summer, Snake River fall, upper Columbia River spring, and upper Willamette River (Ford, 2011). These Chinook salmon subgroups display diverse life-history variation, including the timing of adults returning to freshwater (indicated by season [i.e., spring, summer, or fall] in subgroup names (e.g., Snake River fall) and age of ocean entry for juveniles (fall runs have subyearling [age 0.0] smolts, spring runs have yearling [age 1.0] smolts, and smolt age of summer runs vary by group) (Myers et al., 1998). There is no recognized pink salmon (*O. gorbuscha*) population in the Columbia River basin, although individuals often are observed (Hard et al., 1996; Gustafson et al., 2007). Because of these listings, considerable time and resources have been devoted to defining and implementing actions that will help restore salmon populations in the Columbia River.

Hatchery production of anadromous Pacific salmon in the Columbia River basin is extensive; the Fish Passage Center's (FPC) database indicates that ~140 million salmon smolts were released annually during 2007–10 (FPC data available at http://fpc.org/, accessed July 2011). These hatchery fish support commercial, tribal, and recreational fisheries in marine waters from Alaska to California, in addition to fisheries in the Columbia River (PFMC, 2011). Hatchery fish also dominate adult returns and contribute 34–50% of fall Chinook salmon to more than 80% of spring and summer Chinook and coho salmon returns to the Columbia River (NRC, 1996; ISAB[1]). With the emphasis on restoring wild populations, there is increasing concern about potentially negative effects of hatchery fish on wild populations (NRC, 1996; Rand et al., 2012). However, little is known about these interactions in migratory corridors or estuaries, where hatchery and wild populations that are spatially segregated in stream environments have opportunities to interact (Naish et al., 2008; Rand et al., 2012). This gap in knowledge is particularly notable in open-water habitats of the Columbia River estuary, where such basic information, such as the seasonal presence, relative abundance, or potential size differences between hatchery and wild juvenile salmon, is lacking.

As part of the effort to restore Columbia River salmon, attention is increasingly focused on salmon when they are present in the estuary (Fresh et al., 2005; Bottom et al., 2005, 2006). The estuary phase and the initial ocean stage are viewed as "critical periods" of the salmon life cycle because they are periods of high mortality as salmon transition from freshwater to marine habitats (Pearcy, 1992; Schreck et al., 2006; Welch et al., 2008). For example, Kareiva et al. (2000) estimated that even minor (5%) improvements in estuarine and early ocean survival would reverse population declines in Columbia River spring and summer Chinook salmon. However, the causes for the mortality (e.g., predation, starvation, and disease) or the factors that increase or depress mortality in a given year are largely unknown. Furthermore, juvenile salmon are not the only fishes inhabiting estuaries, but rather they are minor members of a larger fish assemblage (Haertel and Osterberg, 1967; McCabe et al., 1983; Bottom and Jones, 1990). Therefore, understanding processes such as predation on juvenile salmon requires understanding the dynamics of the larger fish community (Saunders et al., 2006). A lack of such information has greatly frustrated managers who must identify actions that can be implemented to increase survival during this critical stage.

Although mortality may be high in the estuarine environment, estuaries provide juvenile salmon with productive foraging opportunities, refuge from piscine predation (especially compared with marine waters), and offer intermediate environments during the physiological transition to salt water (Simenstad et al., 1982; Thorpe, 1994; Bottom et al., 2005). However, the degree of benefit likely varies by species and life history type, because some groups (e.g., subyearling Chinook salmon) make prolonged use of estuaries, whereas others (e.g., steelhead) largely pass through estuaries in a few days (Dawley et al.[2]; Schreck et al., 2006; Campbell, 2010; Roegner et al., in press). Extensive research efforts in the Columbia River estuary from the late 1960s (Johnsen and Sims, 1973) to the mid-1980s (McCabe et al., 1983; Dawley et al.[2]; Bottom and Jones, 1990) clearly established that most juvenile salmon migrating as yearlings (i.e., yearling Chinook and coho salmon and steelhead) passed rapidly through the estuary in the deep channels, bisecting an otherwise broad, flat estuary, where they were effectively caught with a purse seine. By contrast, most subyearling migrants (subyearling Chinook and chum salmon) occupied shallow waters close to shore. Most research efforts conducted since the 1980s have focused primarily on subyearling salmon in shallow-water habitats of the Columbia River estuary (e.g., Bottom et al., 2005; Craig, 2010; Roegner et al., 2010a, in press; Spilseth and Simenstad, 2010).

In 2007, we re-initiated a study the estuarine fish assemblage in deep (~10 m) waters of the Columbia River estuary to address the deficiency of information in these habitats. Specifically, we wanted to characterize the presence and dynamics of juvenile salmon and the greater fish assemblage to which they belong during the spring salmon outmigration (mid-April through late June) and to explore if or how environmental variation may influence the patterns we observed. We were particularly interested in the determination of the following aspects of salmon in the Columbia River estuary: 1) species- or age-class-specific timing and abundance of juvenile salmon and their variation, 2) origins of juvenile salmon, with respect to both hatchery or wild origin, and geographic sources, 3) size distribution and condition of each species or age class of salmon and whether there were size differences between hatchery and wild fish, 4) composition and dynamics of other fishes sharing these open water habitats, and 5) the suitability of nonsalmonids as alternative prey for salmon predators based on overlap in size. Given the multitude of changes that have occurred in the Columbia River basin and estuary over the last 30 years (e.g., Sherwood et al., 1990; NRC, 2004), we also wanted to compare our results with those from studies conducted 3 decades earlier. This comparison allows us to identify how juvenile salmon and the larger estuarine fish community may have changed and begins to provide insight regarding expected changes in the future.

[1] ISAB (Independent Scientific Advisory Board). 2011. Columbia River Basin food webs: developing a broader scientific foundation for fish and wildlife restoration. Doc. ISAB 2011-1. [Available at http://www.nwcouncil.org.]

[2] Dawley, E. M., R. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankis, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Final report of research funded by Bonneville Power Administration. [Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112].

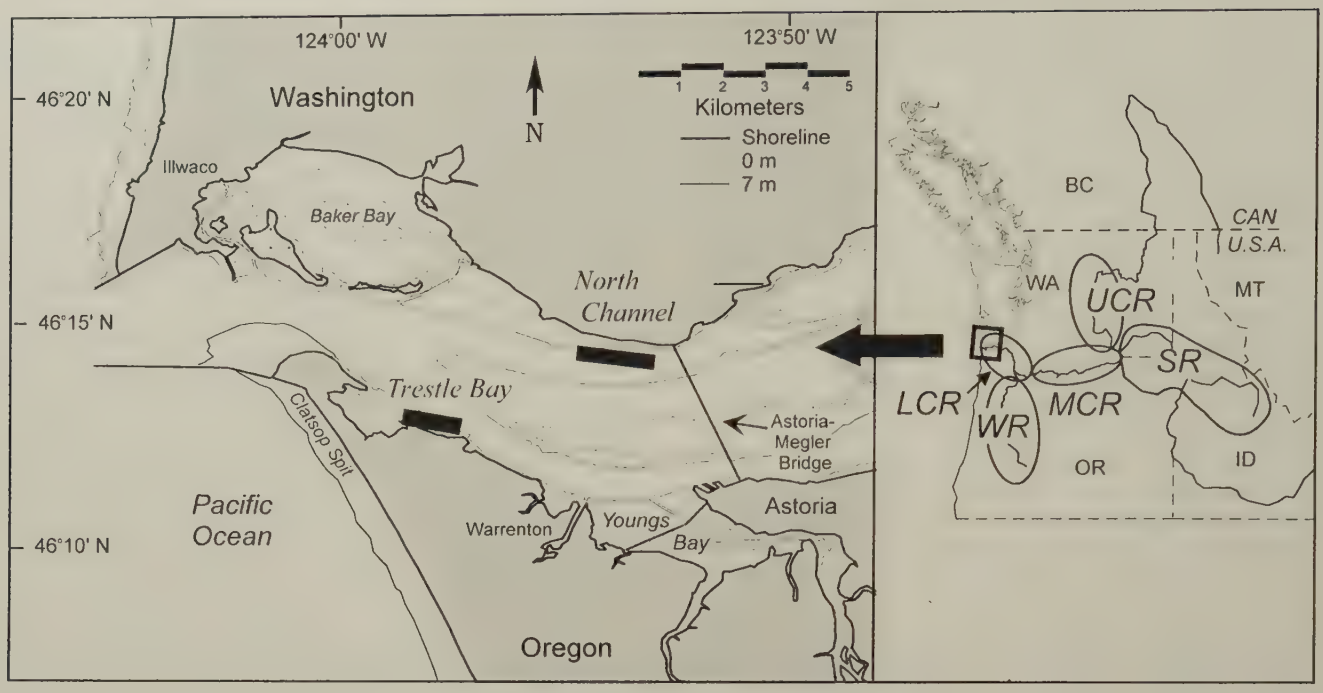

Figure 1

Map of the 2 sampling stations, North Channel and Trestle Bay, used in our study of the estuarine fish assemblage in open-water habitats of the lower Columbia River estuary. Shoreline, 0-m, and 7-m depth contours are indicated, as are major towns. The insert map indicates the location of the study area (black rectangle) and 5 geographic regions within the Columbia River basin from which juvenile salmon originated: lower Columbia River (LCR), Willamette River (WR), mid-Columbia River (MCR), upper Columbia River (UCR), and Snake River (SR). State or province abbreviations: WA=Washington; OR=Oregon; ID=Idaho; MT=Montana; BC=British Columbia.

Materials and methods

Collection of fish

Our sampling was directed toward the spring outmigration of juvenile salmon as they passed through the Columbia River estuary. For each sampling trip or cruise, we had the following objectives: 1) characterize the estuarine fish assemblage by documenting the abundance, size, and condition of fishes (including juvenile salmon) present in the sampling area, and 2) collect 50 individuals of each of 4 juvenile salmon species and age classes (yearling Chinook, subyearling Chinook, and coho salmon, and steelhead) for laboratory analyses; this number reflects a balance between restrictions on lethal sampling of ESA-listed species and the need for sufficient samples for statistical rigor.

To achieve these objectives, fish were sampled during daylight hours every 2 weeks from mid-April to late June or early July during 2007–10 at 2 stations, North Channel (46°14.2′N, 123°54.2′W, river km [rkm 17) and Trestle Bay (46°12.9′N, 123°57.7′W, rkm 13) (Fig. 1). These stations are located in the lower estuary adjacent to the 2 deep channels that bisect the north and south portions of the estuary, respectively, in the "estuarine mixing" region (Bottom and Jones, 1990; Jones et al., 1990). These stations also have historical significance because they have been used as study sites since the late 1960s (Johnsen and Sims, 1973; Dawley et al.[2]).

Sampling was restricted to days with early morning low tides, which typically occur during extreme (minus) tides during springtime; the first set of the net was made at approximately low slack water and sampling continued for the duration of the flood tide. This timetable was adopted because 1) fish are difficult to sample during ebb (outgoing) tides owing to high currents (which often exceed 11 km/h) and 2) strong thermally driven afternoon winds in excess of 48 km/h limited boat maneuverability and, therefore, sampling efficiency. Our timetable left ebb and neap tides and nighttime as times when fish were largely unsampled, but extremely strong downstream currents and close proximity to the hazardous Columbia River bar provide challenging conditions for vessels of any size (Haertel and Osterberg, 1967; Johnsen and Sims, 1973). Nevertheless, in studies of the Columbia River estuary, abundances of juvenile salmon were found to be either greatest during daylight hours (Ledgerwood et al., 1991) or were similar between day and night (Friesen et al., 2007), and therefore we were unlikely to miss large numbers of fish with our sampling schedule.

Fish were sampled with a fine-mesh purse seine (10.6 m deep and 155 m long, with stretched mesh opening 1.7 cm; knotless bunt mesh 1.5 cm); this mesh was sufficiently fine to effectively catch all but a few elongate

fishes (e.g., larval smelt [Osmeridae] and small Pacific sand lance [*Ammodytes hexapterus*]). We restricted sampling to depths of 8–10 m; therefore, the net fished the entire water column. We set the net in 1 of 2 configurations (round hauls or towed), depending on our specific objectives (quantitative catches or maximization of the catch of fish); 2 boats were used in both configurations to deploy and retrieve the net. Quantitative round hauls (n=210) involved setting the net in a circle (area=1913 m^2). We define catch per of unit effort (CPUE) as the abundance of fish per 1000 m^2 (round hauls only), and we tried to complete at least 3 round hauls per station per cruise. When densities of juvenile salmon were low (CPUE<2/1000 m^2), we increased the number of fish caught by towing the net for 8–10 min upstream before closing and pursing the net (n=81 sets). We did not attempt to estimate abundances from these nonquantitative sets but did use the salmon collected during these sets to estimate origin and length–weight relationships, and we used length data from all fishes caught.

Regardless of the set configuration, once the net was pursed and fish had been crowded into the knotless bunt, they were transferred to large (190-L) buckets with running river water. All nonsalmonid fishes were identified to species (Eschmeyer et al., 1983; Hart, 1973) and enumerated, and all but 30 of each species were released. The retained fishes were anaesthetized with tricaine methane sulfonate (MS-222), measured (fork length [FL] or total length [TL] to the nearest 1 mm as appropriate), allowed to fully recover, and then released. Fewer individuals (up to 30) of nonsalmonid species were measured from each set than of salmonids (up to 100) because the focus of our study was on juvenile salmon. The measurement of 30 individuals of each nonsalmonid species provided adequate sample sizes (722–3674 length measurements for commonly caught species across the 4 years) without being overly time consuming. We noted the presence of invertebrates in our catch (e.g., California bay shrimp [*Crangon franciscorum*], Dungeness crab [*Cancer magister*], and jellyfishes [*Aequorea* spp., *Aurelia* sp., *Chrysaora fuscescens,* and *Eutonina indicans*]) but did not attempt to quantify their abundances. All invertebrates that we encountered are believed to be native to the Pacific Northwest, with the possible exception of *Aurelia* sp. (Kozloff, 1987; Wrobel and Mills, 1998).

In the case of extremely large catches (>5000 individuals), the total volume of fish in the net was visually estimated: 3 subsamples of known volume (5500 cm^3) were collected and transferred to separate buckets, and the remaining fish were released directly from the net without having been taken on board the vessel. Fish in each subsample were then identified to species, enumerated, and measured as described above. We estimated the total abundance of each species in the haul by taking the average density of each species across the 3 subsamples and multiplying it by the estimated total volume of fish.

Juvenile salmon were anaesthetized, identified to species, checked for the presence of tags (passive integrated transponder [PIT], visible implant elastomer, coded wire tags [CWTs]), or clipped adipose fins, and measured (FL to the nearest 1 mm). Juvenile salmon that were not needed for laboratory analyses were allowed to fully recover and released; tag codes of individuals tagged with PIT tags were "read" electronically before release. Salmon that were retained were given a lethal dose of MS-222, checked for tags and clips, and measured as above; then, they were individually tagged, bagged, and immediately placed on ice. Once on shore, these fish were transferred to a –80°C freezer for later laboratory analysis. In the laboratory, thawed juvenile salmon were remeasured (FL to the nearest 1 mm), weighed (total wet weight in grams), and rechecked for tags and clip marks. Snouts were removed from fish with CWTs for extraction (see the next section *Origins of juvenile salmon*).

Juvenile Chinook salmon were segregated into 2 age categories: subyearling (age 0.0) or yearling (age 1.0) on the basis of fish length (Dawley et al.[2]). The length dividing subyearling from yearling Chinook salmon ranged from 115 mm FL in April to 140 mm on July 1; it was developed from 1) seasonally adjusted length-frequency histograms (Hinton[3]), 2) known ages based on scale analysis (Fisher[4]), and 3) known ages determined from PIT tags or CWTs.

Origins of juvenile salmon

We estimated the hatchery or wild origins and geographic sources of juvenile salmon. Most of the ~140 million hatchery-origin Pacific salmon released in the Columbia River basin annually during the period of 2007–10 were externally marked by clipping (i.e., amputating) the adipose fin before release. These basinwide percentages of hatchery marking ranged from 67.8% (coho salmon) to 91.9% (yearling Chinook salmon) (FPC database). However, because of the large number of hatchery-produced fish that were unmarked (e.g., 16.7 million subyearling Chinook, 7.2 million coho salmon), individuals with intact adipose fins could either be wild or unmarked hatchery fish. We used annual species-specific mark rates from the FPC online database to estimate the percentage of hatchery fish in our catch (%H), as

$$\%H = \frac{\textit{mark rate in catch}}{\textit{mark rate at hatchery}},$$

where the mark rate in catch = the percentage of marked fish that we observed in the estuary for each species-and-age class in each year.

In cases where mark rates in our catch exceeded those levels reported at hatcheries (i.e., %H>100%), we capped %H at 100% for that year. Because some subyearling

[3] Hinton, S. 2010. Unpubl. data. Northwest Fisheries Science Center, Hammond, OR 97121.

[4] Fisher, J. 2010. Unpubl. data. Oregon State Univ., Corvallis, OR 97331.

Chinook salmon were released from hatcheries after our study period, we considered only releases occurring at least 10 days before our final cruise of the spring: either June 19 (2007, 2008) or June 14 (2009, 2010). This cutoff is conservative (i.e., may underestimate *%H*) because recovery of subyearling Chinook with CWTs (n=127) in our study took an average of 32 days (range: 2–104 days) from time of release at hatcheries.

Extensive fish-tagging programs active throughout the Columbia River basin also provided information about the geographic origins of many individuals collected in the purse seine. In particular, nearly 30 million juvenile salmon (largely of hatchery origin) are tagged with CWTs (Regional Mark Information System [RMIS], database available at http://www.rmpc.org, accessed June 2011) and 2.5 million hatchery and wild salmon are tagged with PIT tags each year (PIT Tag Information System [PTAGIS], database available at http://www.ptagis.org, accessed June 2011). Both tag types provide information about release location and timing; we used this information to estimate the geographic origins of the salmon we collected.

For fish containing either CWT or PIT tags, we extracted the tags, "read" the tag code visually (CWTs) or electronically (PIT tags), and determined the release location from the appropriate online database. To simplify our analysis, release locations were grouped into 5 geographic regions (Fig. 1): below Bonneville Dam (rkm 235, excluding the Willamette River); mid-Columbia River (between Bonneville Dam and the mouth of the Snake River [rkm 522]); upper Columbia River (accessible waters above the confluence with the Snake River); Snake River (all accessible waters of the Snake River); and Willamette River. We could not determine release locations from the few tags (29 CWTs and 2 PIT) that either had no release information (i.e., agency codes or blank tags) or were not in the databases; some CWTs were lost before they could be read.

Environmental data

To gain insight into the environmentally driven dynamics of the estuarine fish assemblage, we recorded both local and regional environmental data for each purse seine set. These 2 environmental data types were expected to reflect different types of variability: local data would vary at very short time scales (minutes to hours) within the estuary, and regional data would represent longer term variability (days to weeks) at larger spatial scales. Our local data consisted of tidal stage and height information for each set and in situ conductivity, temperature, and depth (CTD) profiles made from the surface to the bottom measured before every set of the net. For purposes of this analysis, we used in situ temperature and salinity measurements at the surface (depth of 1 m) and near-bottom (depth of 7 m) to characterize the local water column. Because of equipment problems, CTD casts were not conducted during 2 of our cruises in 2007 (7-1 and 7-6) and 2 cruises in 2008 (8-1 and 8-7; for dates of these cruises, see Table 1). For these 4 cruises, we substituted modeled temperature and salinity data provided by the Center for Coastal Margin Observation and Prediction (Batista[5]); comparisons between modeled data and in situ temperature and salinity measurements indicated that they were highly correlated (coefficient of correlation [r]≥0.82).

We estimated tidal stage (time relative to low tide) for each set on the basis of low tide predicted for Hammond, Oregon, (NOAA station 9439011; http://tidesandcurrents.noaa.gov), which is within 500 m of our Trestle Bay sampling station. We also used this station to predict low tide at the North Channel site because predicted timing of tidal inundation was similar. We used observed (versus predicted) tidal heights recorded at Astoria, Oregon (NOAA station 9439040) because tidal heights were not available for the Hammond station.

We used regional environmental data that characterized both riverine and marine conditions because estuarine fishes likely were influenced by both freshwater and marine environments. Regional riverine data consisted of daily river flow records from Quincy, Oregon (rkm 87; U.S. Geological Survey [USGS] surface water station 14246900; http://www.usgs.gov, accessed August 2011) and daily temperature measurements at the Dalles Dam (rkm 304; USGS surface water station 14105700), both averaged over the days of the cruise. These stations were the nearest to the estuary among the stations where respective data types were collected.

Marine environmental data reflected conditions both near the mouth of the Columbia River and across the North Pacific Ocean. Local marine data included daily sea-surface temperatures (SST) measured at Stonewall Bank (NOAA Data Buoy 46050; 44°38.3′N, 124°32.0′W; http://www.ndbc.noaa.gov, accessed April 2012), daily Bakun upwelling index (UI) for 45°N, 125°W (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling, accessed April 2012), and daily sea-level height (SLH) estimated for Astoria (http://ilikai.soest.hawaii.edu/uhslc/htmld, accessed April 2012). We used 2 indices describing the dominant modes of variability across the North Pacific Ocean at monthly intervals: the Pacific Decadal Oscillation (PDO) index (Mantua et al., 1997; http://www.jisao.washington.edu/pdo) and the North Pacific Gyre Oscillation (NPGO) index (Di Lorenzo et al., 2008; http://www.o3d.org/npgo). We estimated pairwise Spearman correlation coefficients between environmental variables to determine how they were related to each other (Sokal and Rohlf, 1995).

Analytical approach

All analyses were designed to explore how juvenile salmon and the estuarine fish assemblage varied at temporal scales ranging from days to years. Because of our focus on juvenile salmon, our analyses of salmon,

[5] Batista, A. 2012. Unpubl. data. Center for Coastal Margin Observation and Prediction, Oregon Health and Science Univ., Portland, OR 97239.

Table 1

Sampling effort, regional river flow, and river temperature by year and cruise during the 4 years (2007–10) of our study of the estuarine ecology of juvenile salmonids and their associated fish assemblage in open-water habitats of the lower Columbia River estuary. Sampling effort totals, measured as the total number of hauls (round and towed) completed, are provided with dates of each cruise.

Year	Cruise no.	Dates	Total no. of hauls (no. of round hauls)	Mean river flow (1000 m^3/sec)	Mean river temperature (°C)
2007	7-1	17–18 April	8 (8)	8.0	9.3
	7-2	1–4 May	24 (16)	8.7	11.3
	7-3	15–17 May	13 (9)	9.0	13.3
	7-4	30–31 May	14 (11)	7.8	15.0
	7-5	12–13 June	13 (10)	7.9	16.0
	7-6	27–28 June	7 (6)	5.7	17.5
		2007 effort	79 (60)		
2008	8-1	10 April	3 (3)	6.1	7.2
	8-2	23–24 April	12 (6)	7.6	9.0
	8-3	6–8 May	18 (12)	8.3	11.0
	8-4	20 May	7 (6)	13.5	13.5
	8-5	3–5 June	15 (9)	13.9	13.5
	8-6	18–19 June	14 (8)	12.5	14.9
	8-7	30 June–1 July	11 (10)	11.1	17.1
		2008 effort	80 (54)		
2009	9-1	15 April	3 (3)	9.3	8.5
	9-2	23–24 April	15 (9)	9.9	9.7
	9-3	7–8 May	13 (10)	11.2	10.3
	9-4	21–22 May	10 (8)	11.1	13.3
	9-5	4–5 June	13 (9)	11.3	15.4
	9-6	23–24 June	8 (7)	8.2	17.1
		2009 effort	62 (46)		
2010	10-1	13–14 April	14 (9)	7.9	9.3
	10-2	28–29 April	12 (6)	7.7	11.5
	10-3	11–12 May	10 (10)	7.4	11.9
	10-4	25–26 May	9 (7)	8.8	13.3
	10-5	8–9 June	12 (6)	13.4	14.4
	10-6	23–24 June	13 (12)	11.6	15.6
		2010 effort	70 (50)		

especially Chinook and coho salmon and steelhead, were more detailed than our analyses of other fishes.

Fish abundance and composition Analysis of temporal and spatial variation of the estuarine fish assemblage was restricted to catch data collected from round hauls (n=210). Seasonal changes in abundance for each of 6 juvenile salmon species-and-age classes (subyearling and yearling Chinook, coho, sockeye, and chum salmon and steelhead) were qualitatively assessed by visually comparing mean CPUE per cruise by year.

For the entire fish assemblage, including juvenile salmon, we calculated the following univariate metrics to assess patterns of abundance: 1) frequency of occurrence of all fish species during each year, 2) mean CPUE and coefficients of variation for the most commonly caught species, and 3) total abundance of all fishes and the relative abundance (as percentage of total) of the most commonly caught fishes, averaged by cruise. Data generated from these analyses were visually compared. These qualitative measures complemented multivariate techniques, specifically: 1) direct comparisons of subsets of Bray-Curtis similarity coefficients among hauls to examine fine-scale temporal and spatial influence, 2) nonmetric multidimensional scaling (MDS) by haul and cruise, and 3) analysis of similarities (ANOSIM, a multivariate analog for analysis of variance, ANOVA) to test for the influence of temporal variation. All multivariate analyses were run with PRIMER-E[6] software (PRIMER-E Ltd., vers. 6, Ivybridge, U.K.).

[6] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Multivariate analyses were based on pairwise Bray-Curtis similarity coefficients calculated between hauls or cruises. Bray-Curtis similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale (e.g., with percentage or proportions) or the number of variables (e.g., species or hauls) used and produce a value of zero when both values being compared are zero (joint absence problem) (Clarke, 1993; Legendre and Legendre, 1998). In this application, similarity coefficients ranged from 0 (no catches in common) to 1 (identical catches). The fish assemblage used in multivariate analyses was restricted to 13 species-and-age classes of fish that were effectively captured by the purse seine because they were pelagic. We deliberately excluded demersal species from our analyses (e.g., flat fishes [Pleuronectidae], gunnels [Pholidae], and sculpins [Cottidae]) because they were unlikely to be effectively sampled with a purse seine (Bottom and Jones, 1990). The 13 species included the 6 species-and-age classes of juvenile salmon, plus American shad (*Alosa sapidissima*), longfin smelt (*Spirinchus thaleichthys*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), shiner perch (*Cymatogaster aggregata*), surf smelt (*Hypomesus pretiosus*), and threespine stickleback (*Gasterosteus aculeatus*). In these analyses, abundances of each species-and-age class in the 210 round hauls were transformed by using $\log(x+1)$. All species are native to the Columbia River and Pacific Northwest, with the exception of American shad (Hart, 1973; Eschmeyer et al., 1983; Hasselman et al., 2012a).

We compared pairwise Bray-Curtis similarity coefficients calculated among subsets of the 210 round hauls to explore fine-scale spatial and temporal variation in catches. Specifically, we examined spatial variation by comparing pairwise similarities among catches at the 2 stations, correcting for tidal stage (i.e., hauls occurred within 1 h of each other, where time 0 is at low tide) within the same cruise; differences were tested with the Mann-Whitney (MW) test for difference in medians. We explored fine-scale temporal variation by testing Bray-Curtis similarity coefficients among hauls made at the same station and within the same cruise but grouped by tidal stage at 1-h increments (i.e., within 1 h of low tide, 2 h, etc.). We used the Kruskal-Wallis (KW) one-way ANOVA on ranks followed by KW multiple-comparison test to determine which groups were different from the others (Zar, 1984).

We also used the matrix of Bray-Curtis similarity coefficients calculated either among hauls or cruises to construct MDS plots to graphically explore variation in fish assemblage structure at the 2 scales (hauls or cruises). The MDS ordination technique places all points in MDS space in relation to their similarity (i.e., points farther apart in MDS space are less similar than those points closer together). In all MDS analyses, random starting locations were used for each of 25 iterations to find the best solution; minimum stress was attained in multiple iterations which suggest a true minimum solution. Stress values of <0.20 indicate that spatial representation of data by the MDS plot is consistent with the structure of the original data set (Clarke and Gorley, 2006). Finally, we quantitatively evaluated temporal variation in assemblage composition by either haul or cruise, using year and biweek (where biweek 1=April 15–30, 2= May 1–15, etc.) for both analyses and Julian date and time after low tide for the matrix based on hauls. For this analysis, we used ANOSIM, which produces Global R values that indicate the degree of separation of groups generated by a particular factor (or pair of factors). These Global R values range from 0 (no separation) to 1 (complete separation); the program also generates statistical probabilities by permutation.

Environmental variation We evaluated the response of the pelagic fish assemblage to environmental variation at 2 scales: haul and cruise. For the former (haul), we used both local (in situ temperature and salinity measured at depths of 1 and 7 m, and tidal stage and height) and regional (river flow and temperature, SST, SLH, UI, PDO, and NPGO) environmental parameters, whereas for the latter (cruise) we used only regional environmental parameters. For both analyses, environmental parameters were normalized, and then Euclidean distances between hauls or cruises were calculated in environmental multivariate space. The relative difference between environmental conditions for each haul or cruise was then compared to haul- or cruise-specific Bray-Curtis similarity coefficients for the fish community (see above) with the BEST function in PRIMER-E (Clarke and Gorley, 2006). This function creates matrices from different combinations of environmental variables and then compares the order (rank) among the fish assemblage with the environmental matrices to determine the environmental matrix with the highest correlation; statistical significance is estimated by permutation.

Size comparisons We compared size distributions of fishes for 2 reasons: 1) to determine which fish species were similar in size to juvenile salmon and, therefore, might serve as alternative prey for salmon predators, and 2) to examine seasonal and interannual variation in juvenile salmon size. We did not compare the sizes of nonsalmonids between years because measurements were made on fish of multiple, undetermined ages; therefore, interpretation of potentially detectable size differences in length would be complex (i.e., could result from changes in growth or age composition).

We evaluated the length of each juvenile salmon species-and-age class in 4 ways: 1) among years, 2) across the season (by date), 3) among years with weight as a covariate, and 4) between marked (known hatchery) and unmarked (hatchery and wild) fish by cruise. Length and weight data were transformed with $\ln(x+1)$ in all comparisons. We used one-way analysis of variance (ANOVA) to evaluate interannual variability in mean length among years, and two-way ANOVA to examine size differences of clipped (hatchery) or unclipped (hatchery+wild) fish by cruise (Zar, 1984). We used analysis of covariance (ANCOVA) to evaluate seasonal

changes in length (collection date as a covariate) and length–weight relationships (weight as a covariate).

Results

Environmental conditions

Environmental conditions were extremely variable during our study period (mid-April to late June or early July) among the 4 years, because of both daily tidal inundation and extremely high river-flow events (>14,000 m^3/s) in May 2008 and June 2010 (Table 1); flows during May 2008 were the highest observed in more than a decade (USGS National Water Information System, http://waterdata.usgs.gov, accessed Aug 2011). Both high flow events were characterized by rapid increases in flow, but flows remained elevated much longer in 2008 than they did in 2010, resulting in 3 cruises in 2008 during which mean river flow exceeded 12,500 m^3/s compared with only 1 cruise in 2010 with rates that high (Table 1). By contrast, river flow never exceeded 11,600 m^3/s in either 2007 or 2009. River flow also was negatively correlated with the PDO (r=–0.48, P<0.05), indicating the influence of large-scale climate forces on terrestrial environments as expressed by river flow (Lawson et al., 2004).

River temperature measured both at the Dalles Dam and at 1-m depth in the estuary were quite similar (Spearman r=0.98, P<0.05), seasonally increasing from <10°C in mid-April to 15–17°C by late June (Table 1). They also were correlated with coastal SST (r=0.85, P<0.05), which displayed similar seasonal increases. The snowmelt-driven high flow event in 2008 delayed the seasonal increase in temperature, resulting in temperatures that were somewhat lower in June 2008 than in other years. In situ temperatures measured at 7-m depth also were positively correlated with upstream river temperature (r=0.88, P<0.05) and coastal SST (r=0.78, P<0.05), but they were negatively correlated with 7-m salinity (r=–0.38, P<0.05), indicating intrusion and mixing of consistently cold (8–12°C) marine water at depth.

In contrast to surface temperatures, in situ salinity measured before each haul changed dramatically with tidal stage, such that salinities ranged from essentially fresh (salinity<1 psu) to largely seawater (>25 psu) within the 5–7 h of sampling each day. This tidal variation was greatest at 7-m depth, and time elapsed since low tide was a reasonably good predictor of 7-m salinity (linear regression, coefficient of determination, r^2=0.7, P<0.05), but river flow was not (r^2=0.3, P<0.05). However, salinities measured at 1-m depth were influenced both by tidal cycle and river flow, with maximum salinity measured at a depth of 1 m during a cruise being negatively related to flow (r^2=0.5, P<0.05). In particular, maximum salinities recorded at 1-m depth when flow exceeded 10,987 m^3/s were significantly lower (mean=3.5 psu) than values recorded when river flow was below that level (mean=10.2 psu). This pattern suggests that high flows result in water column stratification with a surface layer of largely fresh water.

Fish catches and composition

We completed a total of 291 purse seine sets (210 round and 81 towed) during spring of 2007–10 (Table 1). During these 4 years, we caught an estimated 248,822 fish in round purse seine sets and an additional 58,194 fish in purse seine tows. These fish represented 27 species (Table 2), including all Pacific salmon species present in the Columbia River: Chinook, coho, chum, and sockeye salmon, steelhead, and sea-run cutthroat trout (*O. clarki*). We also documented the presence of 3 species of smelts (whitebait, longfin, and surf), 3 clupeids (Pacific herring, Pacific sardine [*Sardinops sagax*], and American shad), and 3 flatfishes (English sole, starry flounder [*Platichthys stellatus*], and sand sole [*Psettichthys melanostictus*]). Most fishes were present only in juvenile stages, although several species, including most of the forage fishes (e.g., northern anchovy, Pacific herring, longfin and surf smelts, and American shad), threespine stickleback, Chinook salmon, and steelhead, were present as both juveniles and adults.

Catches of individual species-and-age classes were highly variable both among species and years, as indicated by frequencies of occurrence (FO, Table 2) and coefficients of variation (CVs, Table 3), and likely reflected in part whether species were largely resident in the estuary, transitory, or migratory (anadromous). For example, 2 species—surf smelt (transitory) and threespine stickleback (resident)—were caught in almost every set (FO>80%). Other species caught fairly frequently included shiner perch, longfin smelt, Pacific herring, and American shad. Juvenile salmon exhibited varying levels of occurrence, with Chinook and coho salmon and steelhead caught in roughly half of all sets (FO=34–65%), whereas both chum and sockeye salmon were encountered less frequently (FO<24%). By contrast, many species were infrequently observed in our catches, including 15 species that were completely absent in at least one year (Table 2). Mean annual CVs, estimated for the most commonly caught species ranged from 47% (surf smelt in 2010) to 240% (northern anchovy in 2008), with juvenile salmon generally having lower CVs (range: 46–167%) than most species except surf smelt and threespine stickleback. Accordingly, the abundances of even our most commonly caught fishes were highly variable among sets.

Despite this fine-scale variability in abundances, however, the catch of fish each year generally followed a pattern of increasing abundance and species diversity as the spring advanced (Fig. 2). In all years except 2007 (which had higher overall abundances), mean CPUE (number/1000 m^2) per cruise was <50 in mid-April, increased to roughly 500 in May, and dropped slightly in June to 300. The seasonal change in abundance was accompanied by a change in species composition (Fig. 2B): in all years, the estuarine fish assemblage was dominated by threespine stickleback in April, becoming more diverse and variable in May and June with sporadically high relative abundances of northern

Table 2

Frequency of occurrence (%) for all fish species caught in open waters of the lower Columbia River estuary by year during our study during 2007–10. Life history stages: j=juvenile, a=adult, or subadult, with the "0" and "1" indicating subyearling and yearling Chinook salmon ages, respectively. If no life history stage is indicated, a mixture of ages were observed.

Common name	Scientific name	2007	2008	2009	2010
American shad	*Alosa sapidissima*	66.7	74.5	76.1	70.6
Chinook salmon (j, 0)	*Oncorhynchus tshawytscha*	63.3	58.2	63.0	49.0
Chinook salmon (j, 1)	*Oncorhynchus tshawytscha*	41.7	52.7	58.7	49.0
Chinook salmon (a)	*Oncorhynchus tshawytscha*	3.3	0.0	0.0	0.0
Chum salmon (j)	*Oncorhynchus keta*	15.0	23.6	21.7	23.5
Coho salmon (j)	*Oncorhynchus kisutch*	45.0	40.0	47.8	37.3
Cutthroat trout	*Oncorhynchus clarki*	1.7	1.8	0.0	3.9
English sole (j)	*Parophrys vetulus*	3.3	10.9	6.5	5.9
Kelp greenling (j)	*Hexagrammos decagrammus*	1.7	10.9	4.3	0.0
Lingcod (j)	*Ophiodon elongatus*	1.7	5.5	0.0	0.0
Longfin smelt	*Spirinchus thaleichthys*	16.7	16.4	23.9	7.8
Northern anchovy	*Engraulis mordax*	25.0	10.9	15.2	31.4
Pacific herring	*Clupea pallasii*	61.7	30.9	50.0	31.4
Pacific lamprey (a)	*Lampetra tridentata*	0.0	0.0	4.3	0.0
Pacific sand lance	*Ammodytes hexapterus*	0.0	1.8	0.0	0.0
Pacific sardine	*Sardinops sagax*	3.3	0.0	0.0	9.8
Pacific staghorn sculpin	*Leptocottus armatus*	1.7	0.0	13.0	3.9
Pacific tomcod (j)	*Microgadus proximus*	0.0	5.5	0.0	0.0
River lamprey (j)	*Lampetra ayresii*	3.3	5.5	0.0	11.8
Saddleback gunnel	*Pholis ornata*	1.7	3.6	2.2	2.0
Sand sole (j)	*Psettichthys melanostictus*	1.7	0.0	2.2	0.0
Shiner perch	*Cymatogaster aggregata*	30.0	45.5	47.0	21.6
Snake prickleback	*Lumpenus sagitta*	0.0	0.0	4.3	0.0
Sockeye salmon (j)	*Oncorhynchus nerka*	13.3	5.5	4.3	17.6
Sockeye salmon (a)	*Oncorhynchus nerka*	0.0	0.0	0.0	2.0
Starry flounder	*Platichthys stellatus*	1.7	3.6	0.0	5.9
Steelhead (j)	*Oncorhynchus mykiss*	35.0	34.5	52.2	56.9
Steelhead (a)	*Oncorhynchus mykiss*	3.3	0.0	2.2	2.0
Surf smelt	*Hypomesus pretiosus*	86.7	83.6	82.6	86.3
Threespine stickleback	*Gasterosteus aculeatus*	81.7	87.3	91.3	82.4
Whitebait smelt	*Allosmerus elongatus*	0.0	1.8	0.0	0.0

anchovy (especially in 2007 and 2010), Pacific herring (2007 and 2009), surf smelt (2008 and 2009), American shad (2008), and threespine stickleback (2008–10). This pattern of high relative abundance in particular years was associated with high absolute abundances of northern anchovy, Pacific herring, and surf smelt (Fig. 2), whereas variable abundances of threespine stickleback and American shad occurred despite consistent absolute abundances among years (Table 3). Juvenile salmonids were typically minor members of the estuarine assemblage (contributing <5% numerically), except in early May 2010 (cruise 10-3), when their contribution reached 39% of all fish caught. As with threespine stickleback and American shad, their absolute abundances were quite consistent among years.

Multivariate assemblage analyses Results of the multivariate assemblage analyses were consistent with the patterns described above: they indicated high variability at fine temporal scales (among hauls), and less variability at larger temporal scales (among cruises) or at spatial scales (between stations). For example, comparisons of specific subsets of pairwise Bray-Curtis similarity coefficients based on tidal stage or sampling station indicated that the fish assemblage of the Columbia River estuary was extremely dynamic at fine temporal scales (hours) and less dynamic in space. In particular, pairwise similarities calculated among hauls made at the same station and on the same day (311 comparisons) exhibited nearly as much variation (range: 0– 89.3%) as we saw between any 2 hauls across the entire 4 years of study (range: 0–98.8%). Furthermore, similarity coefficients were highest for hauls made close together in time (relative to low tide) and declined with increasing time between hauls. Specifically, mean pairwise similarities among hauls conducted within 1 h of each other (mean=64.0%), were greater than similarities for hauls occurring 1–2 h apart (61.3%), with the lowest mean

Table 3

Mean catch per unit of effort (CPUE, number/1000 m^2) and coefficients of variation (CV; %) estimated by cruise and averaged by year for the most commonly caught fish species in our study in open-water habitats of the lower Columbia River estuary. Also indicated is the rank of each species based on mean abundances averaged across years (1=most abundant).

		Year							
		2007		2008		2009		2010	
Species-and-age class	Rank	CPUE	CV	CPUE	CV	CPUE	CV	CPUE	CV
American shad	5	28.9	165.1	33.5	153.3	26.3	94.5	31.7	110.4
Chinook salmon									
subyearling	7	4.3	98.1	1.7	128.1	4.0	127.3	3.3	113.7
yearling	9	0.6	45.5	0.8	102.1	1.2	106.0	2.4	132.1
Coho salmon	8	1.1	111.0	1.1	166.8	1.6	142.9	1.3	132.6
Northern anchovy	1	1254.9	157.4	1.1	240.4	0.6	125.2	114.9	165.8
Pacific herring	3	295.2	185.3	1.8	173.8	39.9	118.4	0.8	100.5
Shiner perch	6	19.4	183.1	10.4	137.8	10.2	118.4	0.8	127.1
Steelhead	10	0.6	103.5	0.8	165.6	0.8	130.2	1.6	108.3
Surf smelt	4	14.7	54.5	67.2	162.5	30.6	100.1	10.0	47.0
Threespine stickleback	2	88.6	138.0	230.5	127.1	207.7	115.2	102.6	94.4

similarity among hauls made ≥5 h apart (mean=32.7%; KW H=99.6, P<0.05). In addition, pairwise similarities among sets made during the same cruise within 1 h of each other relative to low tide but at different stations (mean=51.5%) were lower than similarities among sets made at the same station (64.0%; MW U=6.9, P<0.05) and comparable with hauls made at the same station but 3–4 h apart. Taken together, these results suggest a highly dynamic estuarine fish assemblage at fine time scales with modest spatial variation.

We also used MDS plots to graphically evaluate variation in the fish assemblage at 2 scales (haul and cruise). This evaluation indicated that at fine time scales (haul) there was little correspondence between the fish assemblage and any time scale (e.g., time after low tide, cruise, biweek, year) or station (Fig. 3B). For example, hauls occurring within any particular 2-week period failed to form obvious assemblage groups but instead more or less spanned the range of MDS space. By contrast, when considered by cruise, there was a fairly clear pattern with the larger time scale (Fig. 3A). Results from the ANOSIM analysis were consistent with patterns observed in the MDS plots, showing better defined groups (i.e., higher Global R values) by cruise than by haul. When each haul was considered independently, no single or pair of variables produced well-defined groups (R<0.40), consistent with the lack of obvious groups in the MDS plot (Fig. 3B). In this analysis, the variable "biweek" produced the best groups (Global R=0.22), and inclusion of year in a 2-factor analysis increased biweek group separation (Global R=0.35) although year itself did not produce well-defined groups (Global R=0.00). When evaluated by cruise, results were similar to those results produced by haul: the single variable biweek provided the greatest group separation (Global R=0.43), and biweek produced more distinct groups (Global R=0.52) when combined with year.

Environmental forcing of assemblage composition We explored the environmental variables that best fitted the fish assemblage data, either by haul or averaged by cruise. When examined by haul, the environmental model producing the best fit (r=0.40, P<0.05) to the species composition data consisted only of in situ 7-m salinity, and models with fits that were only slightly poorer (0.39≤r≤0.40) included 7-m salinity, 1-m salinity, 1-m temperature, and coastal SST (which was correlated with 1-m temperature). These results suggest the fish assemblage is actively responding to environmental forcing at short temporal scales (hours) associated with tidal inundation and to a lesser extent with seasonal changes. The same analysis for fish assemblage averaged by cruise also indicated that the highest correlation occurred with a single variable, river water temperature (r=0.57, P<0.05), which is largely a seasonal signal. Other models with fairly high correlations (0.46≤r≤0.49) with the fish data included river temperature, coastal SST, PDO, and river flow. Given the strong correlations between river temperature and SST, and between river flow and the PDO, these results suggest the fish community is influenced from both types of climate signals: seasonal and river flow.

Juvenile salmon abundance and timing in the Columbia River estuary

Despite high variability in overall catches, the abundance and timing of juvenile salmon in the estuary was surprisingly consistent among years (Fig. 4). In

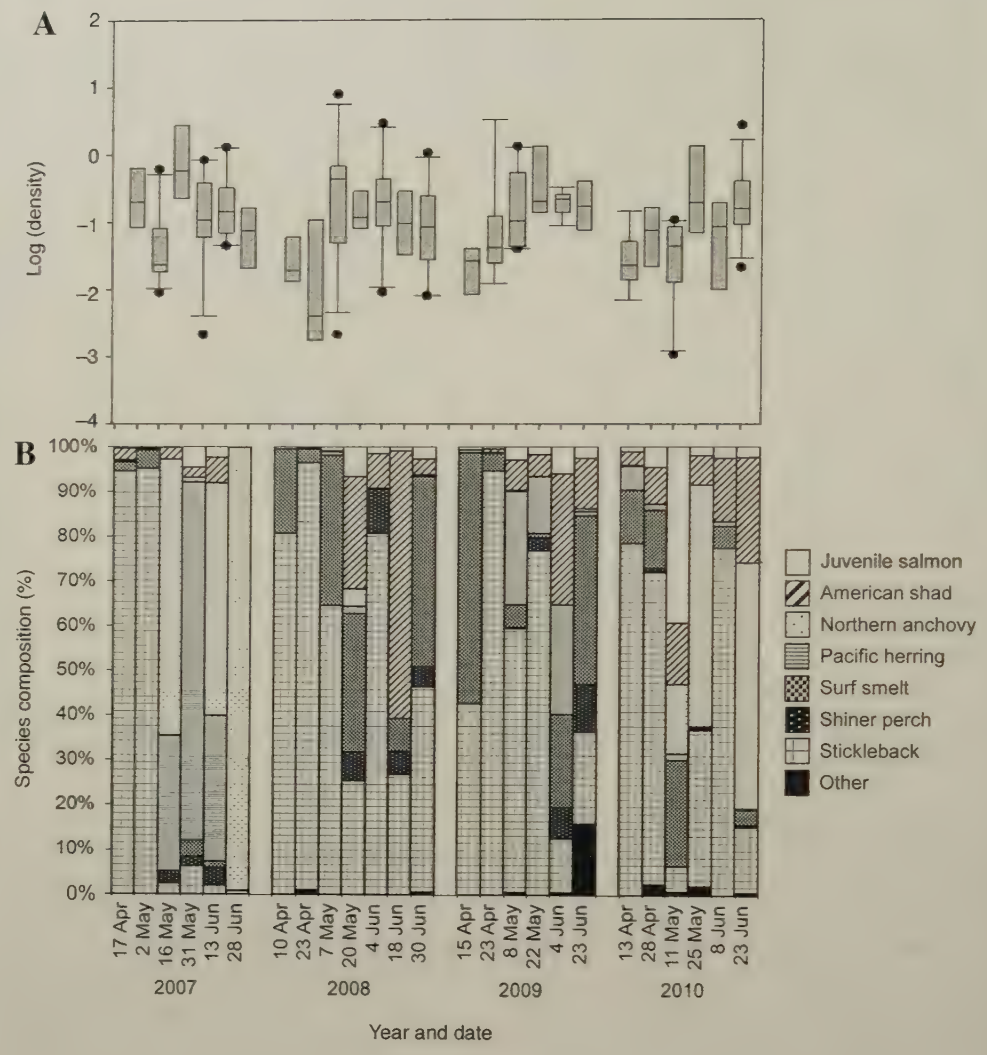

Figure 2

(**A**) Box plots of log-transformed density (number/m^2) and (**B**) percent composition of dominant fish species caught by cruise during spring of 2007–10. These species include American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), shiner perch (*Cymatogaster aggregata*), and threespine stickleback (*Gasterosteus aculeatus*). The category of juvenile salmon includes all species-and-age classes of juvenile salmon combined: yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), sockeye salmon (*O. gorbuscha*), and steelhead (*O. mykiss*). The box plots illustrate 25th and 75th percentiles (lower and upper edges of box, respectively), the median (line within the box), 10th and 90th percentiles (whiskers [error bars] below and above the box, only on cruises when $n \geq 9$), and dots indicate outliers (<10th or >90th percentiles).

mid-April, when sampling began, catches of all juvenile salmon were extremely low (CPUE<1/1000 m^2). As the spring progressed, the abundances of juvenile salmon increased. Maximum abundances occurred in mid-May for yearling Chinook and coho salmon and steelhead, a somewhat earlier peak in abundance occurred in early May for chum salmon, later peaks in abundance occurred in early June for sockeye salmon, and late June or early July for subyearling Chinook salmon. Consequently, when sampling stopped in late June or early July, only subyearling Chinook salmon were still being caught (Fig. 4). The magnitude of peak abundances also exhibited species-specific variation, with the lowest peak abundances observed for chum and sockeye salmon (CPUE<2/1000 m^2), moderate levels seen for yearling Chinook and coho salmon

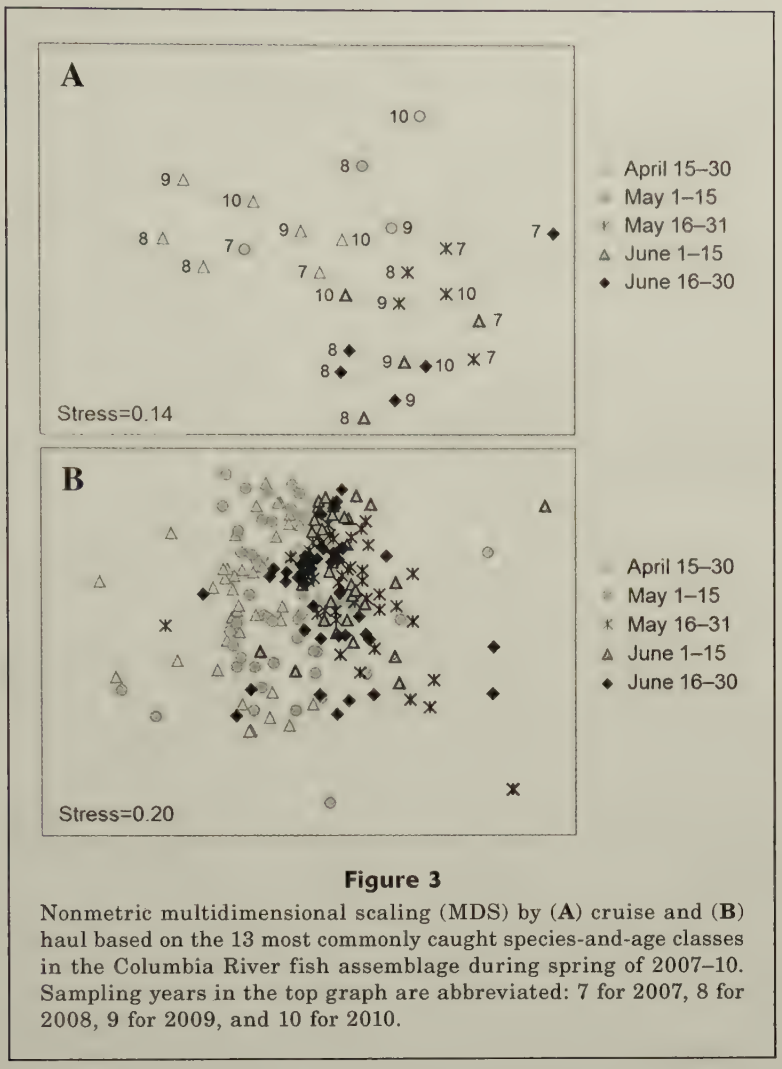

Figure 3

Nonmetric multidimensional scaling (MDS) by (**A**) cruise and (**B**) haul based on the 13 most commonly caught species-and-age classes in the Columbia River fish assemblage during spring of 2007–10. Sampling years in the top graph are abbreviated: 7 for 2007, 8 for 2008, 9 for 2009, and 10 for 2010.

and steelhead (CPUE=2–5/1000 m^2), and the highest abundances estimated for subyearling Chinook salmon (CPUE=8–10/1000 m^2). There was also variation in the length of time that salmon were present in the estuary: both chum and sockeye salmon were caught typically only during a 2–4 week period, yearling Chinook and coho salmon and steelhead were caught readily in the estuary for 6–8 weeks each year, and subyearling Chinook salmon were present for at least 2 months (and presumably longer but sampling was terminated).

We also observed interannual variation in this seasonal abundance pattern, although no single year was associated with exceptional catches for any species-and-age class of juvenile salmon (Fig. 4). For example, the timing of maximum abundances of yearling Chinook and coho salmon and steelhead occurred in late May in 2007 and early May in 2009 and 2010 and subyearling Chinook salmon occurred early in 2009 and 2010 and late in 2008. Similarly, we observed no consistent patterns in the magnitude of maximum abundances; peak abundances for most species, except sockeye salmon, were low in 2007, yet levels were high for chum salmon in 2008, coho salmon in 2009, and steelhead and yearling Chinook salmon in 2010.

Origins of juvenile salmon

We determined the origins of juvenile salmon by both rearing conditions (hatchery vs. wild) and geographic location. From the number of clipped adipose fins we observed in our catches and the number of fish clipped basinwide at hatcheries, we concluded that most juvenile salmon that we collected were of hatchery origin (Table 4); this percentage ranged from 91% for steelhead to 99% for coho salmon, with estimates exceeding 100% for both coho and subyearling Chinook salmon in some years.

We also were able to determine geographic origin for 508 juvenile salmon from which we recovered CWTs and for 38 juveniles with PIT tags (Table 5). These tagged fish originated from locations throughout the Columbia River basin—lower, mid-, and upper Columbia River and the Snake and Willamette rivers. In a notable exception to this pattern, tagged steel-

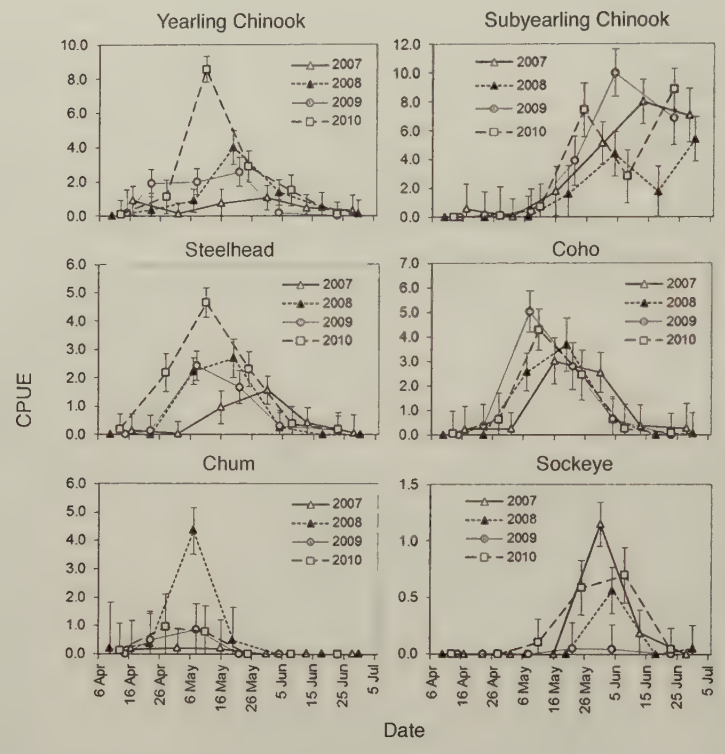

Figure 4

Catch per unit of effort (CPUE) of juvenile salmonids—yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*)—by date and year in the Columbia River estuary during spring of 2007–10; CPUE values are given as number/1000 m^2 ±1 standard error of the mean (SE).

head originated only from the Snake or mid-Columbia rivers (PIT tag) or Snake and upper Columbia rivers (CWTs).

Fish size

Relative length The length of commonly caught fishes in our study varied considerably, from large (>280 mm) American shad and juvenile steelhead to consistently small (<70 mm) threespine stickleback (Fig. 5). Because juvenile steelhead were the largest juvenile salmon, only large American shad were of similar size. In contrast, the length range of coho and Chinook salmon overlapped the size of many commonly caught species, including northern anchovy, Pacific herring, shiner perch and surf smelt. The size range for many fishes (e.g., American shad, surf smelt, and Pacific herring) was quite broad because of mixtures of both juvenile and adult ages in our catches.

Juvenile salmon size The size of juvenile salmon generally varied by year and season, although no clear cross-species (i.e., year-specific) patterns were observed in any of the comparisons. For mean length by year, statistically significant differences among years were observed for all species and age classes ($H \geq 11$, $P < 0.05$), except for coho salmon ($P > 0.10$; Fig. 6). However, these interannual differences were generally small, with absolute mean size differences ranging from 4.7 mm (yearling Chinook) to 11.6 mm (steelhead), which translated to a 3–14% difference in length between years. The mean size of juvenile sockeye salmon showed

Table 4

Estimated percentage of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon and steelhead (*O. mykiss*) of hatchery origin caught in open waters of the lower Columbia River estuary. Hatchery percentages were estimated from the percentage of clipped adipose fins observed in the estuary catches divided by the percentage of clipped fish released from hatcheries, averaged over the 4 years of our study, 2007–10. Also included are the mean number of juvenile salmon released annually and the percentage of fish clipped at hatcheries. Hatchery release numbers and information on clipped fish are from the Fish Passage Center (data available at http://fpc.org/, accessed July 2011). Chinook 0 and Chinook 1 refer to subyearling and yearling age classes, respectively.

	Species-and-age class			
	Chinook salmon 0[a]	Chinook salmon 1	Coho salmon	Steelhead
Hatchery release (millions)	49.5	32.4	22.4	15.0
Percentage clipped at hatchery	75.7	91.9	67.8	85.4
Percentage clipped (observed in estuary)	76.0	86.9	76.9	77.6
Estimated percent hatchery	95.7[b]	94.6	99.0[b]	90.9

[a] Includes only hatchery fish released at least 10 days before the final cruise of the season: before June 19 in 2007 and 2008 and June 14 in 2009 and 2010.

[b] Capped at 100% in some years; therefore, estimated percent hatchery does not equal the percent clipped in estuary divided by percent clipped at hatchery.

Table 5

Geographic origins of Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon and steelhead (*O. mykiss*) caught during spring of 2007–10 in the lower Columbia River estuary, determined on the basis of recovery of coded wire tag (CWT) and passive integrated transponder (PIT) tags, shown by major regions of the Columbia River basin. Chinook 0 and Chinook 1 refer to subyearling and yearling age classes, respectively. No tagged steelhead were released in the Willamette and lower Columbia Rivers.

	Species-and-age class							
	Chinook 0		Chinook 1		Coho		Steelhead	
	PIT	CWT	PIT	CWT	PIT	CWT	PIT	CWT
Number of tags recovered	0	127	27	254	2	87	9	33
Release or tagging region[1]	Percentage of tags recovered by region							
Lower Columbia River		29.9	3.7	5.9	0	54.1	0	0
Willamette River		0	0	4.3	0	1.1	0	0
Mid-Columbia River		48.8	14.8	14.6	0	3.4	11.1	0
Upper Columbia River		0.8	29.6	42.1	100	39.1	0	21.2
Snake River		20.5	51.9	33.1	0	2.3	88.9	78.8

[1] Release or tagging regions: lower Columbia River—below river km (rkm) 235 (Bonneville Dam), excluding the Willamette River; Willamette River—all locations in the Willamette River; mid-Columbia River—between Bonneville Dam and confluence with the Snake River (rkm 522); upper Columbia River—accessible waters above the confluence with the Snake River (rkm 522); Snake River—all accessible waters of the Snake River beginning at rkm 522.

the largest variation (annual means ranged from 104 to 135 mm), but the larger size likely reflects that some fish emigrated as 2-year-old smolts (age 2.0) rather than as yearlings (age 1.0). In addition, when mean size was examined across all years, in any given year at least one species-and-age class of juvenile salmon was the largest and one was the smallest, with the exception of 2008, when no species-and-age classes were the smallest. This result suggests that interannual variability in juvenile salmon size was independent for each group (Fig. 6).

We also observed seasonal changes in the size of juvenile salmon; the seasonal size data, like the annual size data, displayed no cross-species patterns. Both coho and yearling Chinook salmon declined in length as the season progressed, whereas steelhead and subyearling Chinook salmon increased in length. Taking into account this seasonal change in length, the mean size of both juvenile subyearling Chinook salmon and steelhead varied by year (ANCOVA test of means, variance ratio $[F]>8.0$, $P<0.01$), but the size of yearling Chinook and coho salmon did not (ANCOVA test of means, $F\leq1.8$, $P>0.10$). We examined the length–weight relationships of juvenile salmon; common slopes (across all years) between transformed length and weight data ranged from 0.312 for yearling Chinook salmon ($n=658$) to 0.329 for subyearling Chinook salmon ($n=776$), with intermediate slopes for steelhead (0.325, $n=250$) and coho salmon (0.315, $n=637$). Coho salmon and both age classes of Chinook salmon had different slopes between length and weight among years (ANCOVA test of slopes, $F\geq2.3$, $P<0.05$), but, for steelhead, no difference in slope was detected during the 3 years for which data were available (2008–10; $F<1.0$, $P>0.10$).

Finally, we compared the size of clipped (hatchery) and unclipped (wild and hatchery) fish to determine whether clipped hatchery fish were consistently larger than unclipped fish (Fig. 7), as might be the case if most unclipped fish were of wild origin. Examined across all cruises and years, clipped individuals were statistically larger than unclipped fish for coho salmon (mean lengths of 148.7 vs. 140.6 mm, respectively; Two sample $t=6.9$, $P<0.05$) and steelhead (221.6 vs. 198.2 mm, respectively; two sample $t=11.1$, $P<0.05$), but no difference was detected for subyearling or yearling Chinook salmon ($t<1.0$, $P>0.10$). When examined for differences among cruises (to account for seasonal changes in size) the findings were the same: significant differences for coho salmon and steelhead (two-way ANOVA, $F\geq36$, $P<0.05$) but not subyearling or yearling Chinook salmon (two-way ANOVA, $F\leq1.0$, $P>0.10$) (Fig. 7). In addition, we found interaction effects ($F\geq1.8$) for all species at a significance level of $P<0.10$, indicating that although clipped individuals were generally larger than unclipped individuals by cruise, the patterns were not consistent across all cruises.

Discussion

The pelagic fish assemblage we observed in open waters of the lower Columbia River estuary during spring 2007–10 was characteristic of other Pacific Northwest estuaries including those assemblages examined in

earlier studies in the Columbia River (e.g., Haertel and Osterberg, 1967; McCabe et al., 1983; Fox et al., 1984; Bottom and Jones, 1990). Many of these species are also commonly caught in marine waters near the mouth of the Columbia River (Brodeur et al., 2005). All species are native to the Columbia River estuary and the Pacific Northwest, with the exception of American shad. This species was introduced into the Columbia basin from the U.S. Atlantic coast (Wydoski and Whitney, 2003) and is currently the single most abundant anadromous fish species in the Columbia River (Hasselman et al., 2012a).

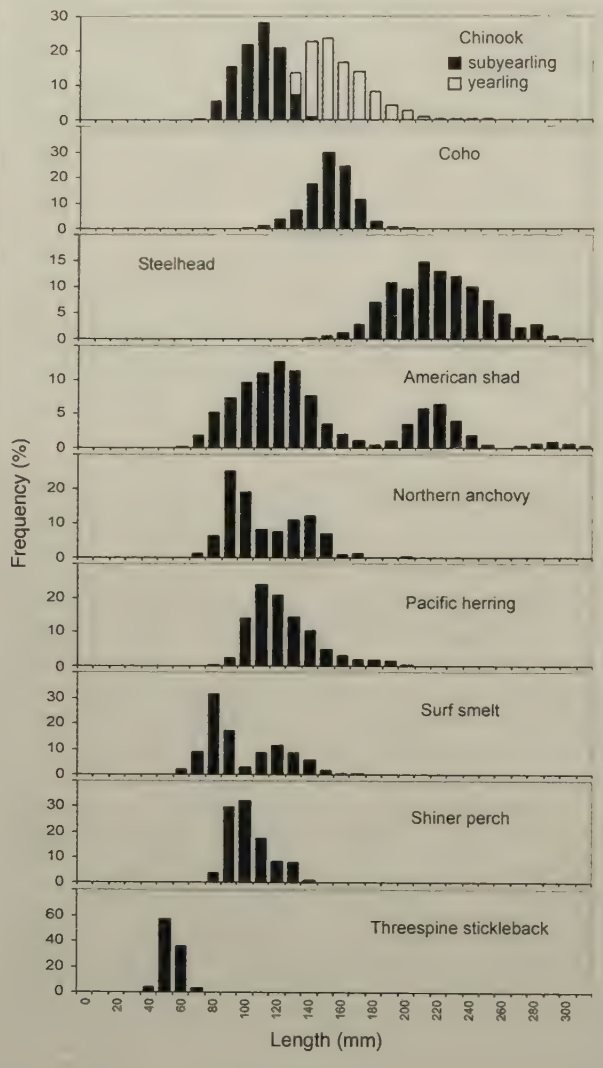

Figure 5

Distributions (%) of length (fork or total; in mm) frequency for selected fish species—Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), shiner perch (*Cymatogaster aggregata*), surf smelt (*Hypomesus pretiosus*), and threespine stickleback (*Gasterosteus aculeatus*)—captured in the Columbia River estuary during 2007–10, all years combined.

The fish assemblage as a whole was extremely dynamic with large variation at daily, seasonal, and interannual time scales. Although there was a general pattern of increasing abundance and species diversity as the season progressed, we often observed nearly as much variation within a single day or cruise as we did within the entire 4 years of our study. Our results indicate that the fish assemblage was responding to environmental forcing at both local (e.g., tide and salinity) and seasonal (e.g., river temperature) time scales. Not surprisingly, this conclusion is similar to the determinations of earlier studies: the fish assemblage was influenced by tides, season, and river flow (Haertel and Osterberg, 1967; Bottom and Jones, 1990; Jones et al., 1990; Simenstad et al., 1990).

Our results are consistent with (and likely in response to) highly dynamic and complex physical circulation in the estuary. Columbia River estuarine circulation is influenced by both riverine processes (e.g., seasonal flow cycles) and ocean processes (e.g., wind-forced upwelling and daily tidal inundation) and their interactions, which result in circulation patterns and water column properties that vary at temporal scales ranging from minutes to years (Jay and Smith, 1990; Chawla et al., 2008; Roegner et al., 2010b). In addition, the north and south channels each have distinct circulation dynamics: strong river flow and a weak salt wedge in the south channel and more salinity intrusion and less river flow in the north channel (Jay and Smith, 1990; Chawla et al., 2008). Given these physical differences between the 2 channels (and, therefore, our study sites), it is surprising that our catches at the 2 stations were not more different than they were.

In addition to physical forcing, variation in the estuarine fish assemblage also reflects use patterns by different species-and-age classes of fish (Bottom and Jones, 1990; Simenstad et al., 1990). For example, many of the species that we caught frequently are typical euryhaline estuarine residents for at least part of their life cycle; this list includes surf smelt, threespine stickleback, shiner perch, longfin smelt, and juvenile Pacific herring and American shad. Primarily marine species (northern anchovy, whitebait smelt, Pacific sardine, lingcod [*Ophiodon elongatus*], and Pacific tomcod [*Microgadus proximus*]) were caught less consistently in the estuary, likely a reflection of seasonal patterns of estuarine use, offshore abundances, and whether conditions in the Columbia River estuary were favorable for occupation (Bottom and Jones, 1990). Finally, many species use the estuary primarily as a migration corridor and were, therefore, consistently caught every year at modest frequencies; downstream migrants include all juvenile salmon and river lamprey (*Lampetra ayresii*), and upstream migrants were adult age classes of American shad, Pacific lamprey (*Lampetra tridentata*), Pacific herring, Chinook salmon, and steelhead.

We observed changes in the fish assemblage in response to high flow events in 2008 and 2010; these

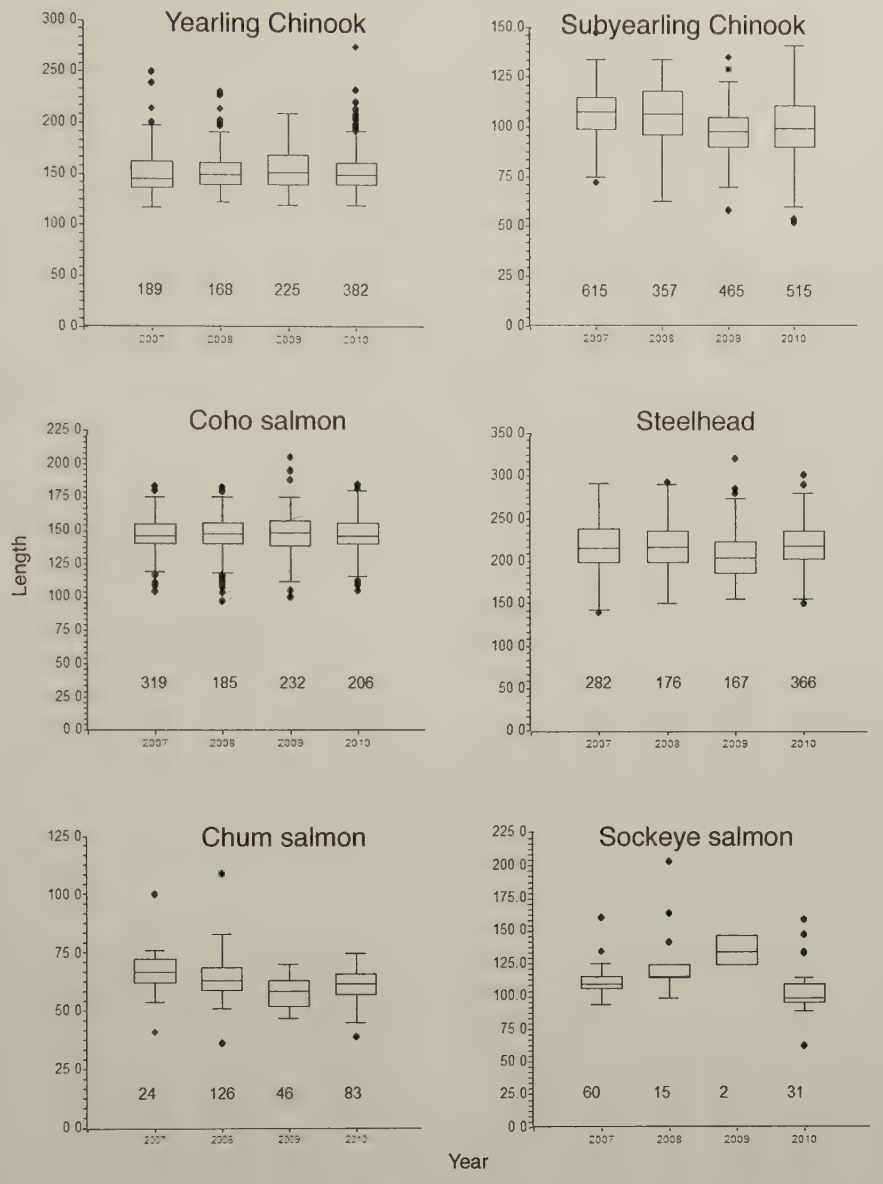

Figure 6

Box plots of fork length (mm) by year for each juvenile salmon species-and-age class: yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*). The box plots illustrate 25th and 75th percentiles (lower and upper edges of box, respectively), the median (line within the box), 10th and 90th percentiles (whiskers [error bars] below and above the box), and dots indicate outliers (<10th or >90th percentiles). Samples sizes are provided below each box. Scales for each graph are different to emphasize species-specific patterns.

events served as natural experiments for the influence of flow. High flow rates influence water column properties and circulation patterns in the estuary (Jay and Smith, 1990; Chawla et al., 2008), including the decline of maximum surface salinity that we observed with increasing flows. Estimated residence time of water in the Columbia River estuary also was much shorter during high flows in 2008 than in 2007, 2009, or 2010 (CCMOP, 2010). High flows also may cause direct, species-specific behavioral responses in fish, including downstream displacement (Dege and Brown, 2004; Purtlebaugh and Allen, 2010). Northern anchovies seem particularly sensitive to high river flows as indicated by their near absence when flows were high in 2008 (cruise 8-4 in

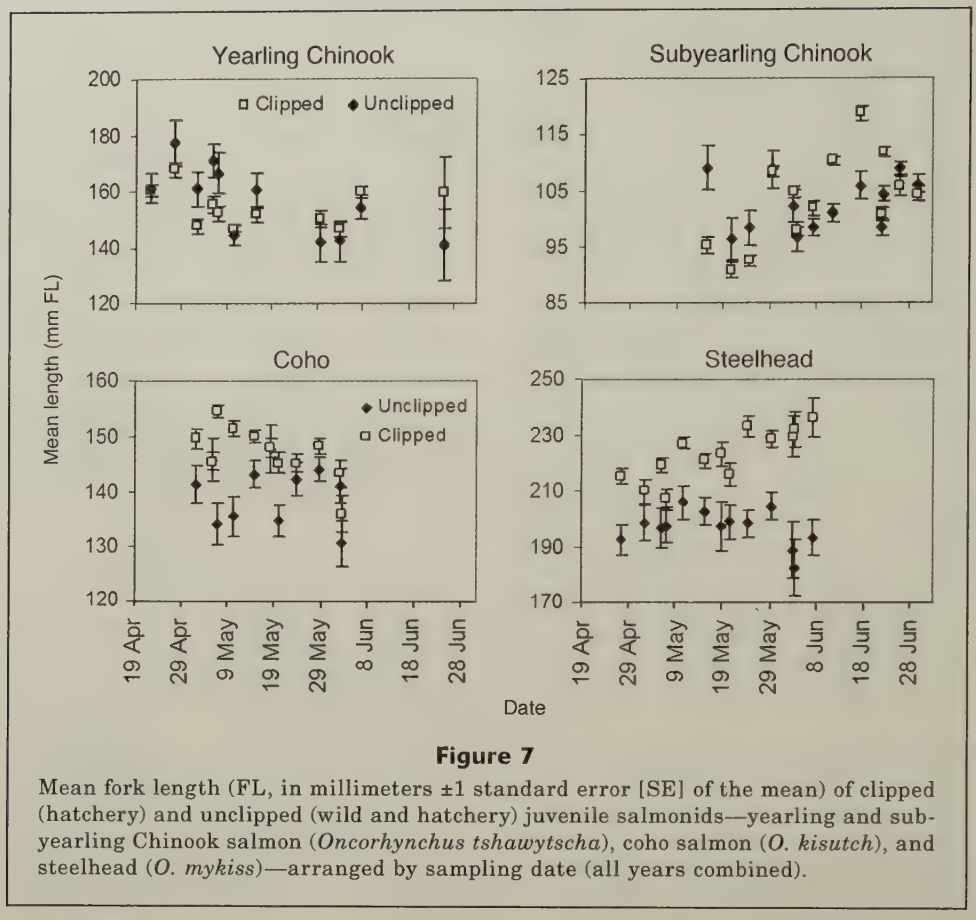

Figure 7

Mean fork length (FL, in millimeters ±1 standard error [SE] of the mean) of clipped (hatchery) and unclipped (wild and hatchery) juvenile salmonids—yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*)—arranged by sampling date (all years combined).

June onwards) and again on 8 June 2010 (cruise 10-5) during the brief high flow event. Northern anchovy are primarily a marine species but move into estuaries from marine waters in the spring and summer (Fox et al., 1984; Bottom and Jones, 1990). We observed daily movement into the estuary with the flood tide; our largest catches (CPUE>300/1000 m^2) of this species occurred an average of 5 h after low tide when both 1-and 7-m salinities were relatively high (5 and 21 psu, respectively). Given the largely marine nature of northern anchovy, we believe the high flows inhibited their entry into the estuary. In contrast, low abundance of northern anchovy in the estuary in 2009, a year with "normal" flow, was likely a result of their low abundance in marine waters off the mouth of the Columbia River during the spring of 2009 (M. Litz, unpubl. data).

We also suspect that high flows may displace juvenile salmon downstream and transport them rapidly through the Columbia River estuary. For example, in the years with normal flow (2007 and 2009), juvenile Chinook and coho salmon and steelhead reached peak abundances on different dates, and they were at modest abundances (CPUE≥2/1000 m^2) for 6–8 weeks. In contrast, in 2008 all yearling fish reached peak abundances on 20 May (cruise 8-4) as the flow was rapidly increasing, with much lower catch rates on the cruise after (but not before) 20 May. This finding suggests that the fish were being flushed downstream. Other research efforts in the Columbia estuary have shown that juvenile salmon initiate migration in response to increasing flows (Coutant and Whitney, 2006) and that migration rates are highest during high flows (Giorgi et al., 1997; Friesen et al., 2007). It currently is unknown whether juvenile salmon might also respond to high flows by moving laterally into shallower water. Because both migration timing and flow rates influence juvenile salmon behavior and survival (Scheuerell et al., 2009; Petrosky and Schaller, 2010), better understanding of these fine-scale processes is essential for conservation and recovery of at-risk salmon populations.

Predation is a likely source of mortality for juvenile salmon in the Columbia River estuary (ISAB[1]). Therefore, knowing who the predators are is essential. We caught several fishes that can be piscivorous as adults (e.g., lingcod and Pacific tomcod; Love, 2011); however, all individuals were juveniles (and often smaller than juvenile salmon) and therefore unlikely predators of juvenile salmon in the estuary. Three potential piscine predators were cutthroat trout and adults of both spring Chinook salmon and steelhead, all of which are highly piscivorous (Quinn, 2005; Duffy and Beauchamp 2008). Whereas cutthroat trout have relatively small populations in the Columbia River (ISAB[1]), both spring Chinook salmon and steelhead have large populations:

during 2007–10, the estimated in-river run size of adult spring Chinook salmon averaged 400,000 fish (PFMC, 2011), and an average of 21,000 steelhead were counted crossing Bonneville Dam between April 15 and June 30 (FPC database). Although adult salmon generally are believed to cease feeding once they enter freshwater (Groot and Margolis, 1991; Quinn, 2005), if they continue to feed while in the Columbia River estuary, their predation effect on juvenile salmon may be considerable. Unfortunately, we were unable to examine adult salmon diets because of restrictions on ESA-listed species. Despite considerable focus on other piscine predators in freshwater regions of the Columbia River (ISAB[1]), this potential predation source has been largely overlooked but clearly deserves further attention.

Several highly visible predators in the Columbia River estuary (e.g., harbor seals [*Phoca vitulina*], California [*Zalophus californianus*] and Stellar [*Eumetopias jubatus*] sea lions, Caspian Terns [*Hydroprogne caspia*], and Double-crested Cormorants [*Phalacrocorax auritus*]) consume many of the fish species we caught in our study (e.g., anchovy, smelt, clupeids, and shiner perch), including juvenile salmon (Collis et al., 2001; Browne et al., 2002; Anderson et al., 2004, Anderson et al., 2007; Lyons et al., 2007). A primary objective of research on avian predators in the Columbia River estuary is to identify factors influencing predation rates on juvenile salmon, including the abundance of alternative prey (Anderson et al., 2007; Lyons et al., 2007). However, these studies have been hampered by a lack of direct measurements of the fish assemblage or information regarding how it varies at seasonal or annual time scales. Our results provide this critical information and even simple comparisons offer unique insight. For example, the size distribution of forage fishes in our study fully overlaps the size distribution of juvenile salmon (Fig. 5), suggesting that forage fishes are appropriate prey for predators focused on fish that are the size of salmon. In addition, the proportions of salmon in the diets of both Caspian Terns and Double-crested Cormorants are consistently highest in early May (Bird Research Northwest [BRN], http://www.birdresearchnw.org, accessed August 2011), at a time when yearling salmon abundance is rapidly increasing (Fig. 4), yet densities of forage fish are still relatively low (Fig. 2). Furthermore, our findings that river flow influences the estuarine fish assemblage were successfully used to relate flow to the diets of Caspian Terns (Lyons, 2010). Future analyses will include comparisons of the abundance and size of fish (both salmon and nonsalmonids) in the environment and in predator diets to gain further understanding of the dynamics of this important predator–prey relationship.

Juvenile salmon in the Columbia River estuary

Compared with high variation in the overall fish assemblage, the seasonal pattern of juvenile salmon abundance was quite consistent between years (Fig. 4, Table 3). These seasonal patterns are similar to the patterns reported in studies conducted in the Columbia River estuary in the late 1970s and early 1980s (Dawley et al.[2]; McCabe et al., 1983; Bottom and Jones, 1990) and typical of other Northwest estuaries (Bottom and Jones, 1990; Groot and Margolis, 1991; Quinn, 2005). We also observed consistency between contemporary migration patterns and those patterns determined before the advent of large-scale hatchery production and other anthropogenic changes in the Columbia River basin and estuary (Sherwood et al., 1990; NRC, 1996). In particular, Burke (2004) analyzed migration patterns of juvenile Chinook salmon through the Columbia River estuary in 1914–16 using data provided by Rich (1920). This early study found that yearling Chinook salmon migrated through the estuary at approximately the same time that we find (peak in mid-May and low in late June), although they (Rich, 1920; Burke, 2004) also observed an earlier abundance peak in March. We did not sample during March; however, we did not observe elevated abundances in mid-April (suggestive of an earlier abundance peak), nor was one apparent in the daily smolt counts at Bonneville Dam that commence each spring in early March (FPC database). The size of these historical yearling migrants (80–125 mm FL; Burke, 2004) also was much smaller than the size we currently observe (Fig. 6), although part of the size difference may result from a different sampling location. Juvenile salmon collected near shore (where Rich [1920] likely collected his fish) tend to be smaller than the ones collected in open waters (senior author, unpubl. data). Our trends for subyearling salmon most closely mirror the "fingerling-estuarine rearing" group described by Burke (2004) that was at low abundance in mid-May, reached peak abundance in mid-July, and continued to be present in the estuary through fall. Like yearling migrants, these historical fish (mean size ~85 mm FL) were smaller than the fish we currently catch, but they also were caught near shore where we expect they would have been smaller.

Similar to our findings, Dawley et al.[7] observed a similar composition of juvenile salmon by species-and age-class by month during 1978–80, with approximately equal abundances of subyearling and yearling Chinook and coho salmon and steelhead in May and mainly subyearling Chinook salmon in June (Fig. 8B). However, in April, we caught more subyearling Chinook salmon and chum salmon than the earlier catches, which had higher levels of yearling Chinook and coho salmon. The higher chum catches that we observed likely reflect a modest increase in the Columbia River chum populations (Ford, 2011). It is not apparent why we observed higher proportions of subyearling Chinook salmon in

[7] Dawley, E. M., R. Ledgerwood, and A. L. Jensen. 1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983: vol. I: Procedures, sampling effort, and catch data. Final report of research funded by Bonneville Power Administration. [Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.]

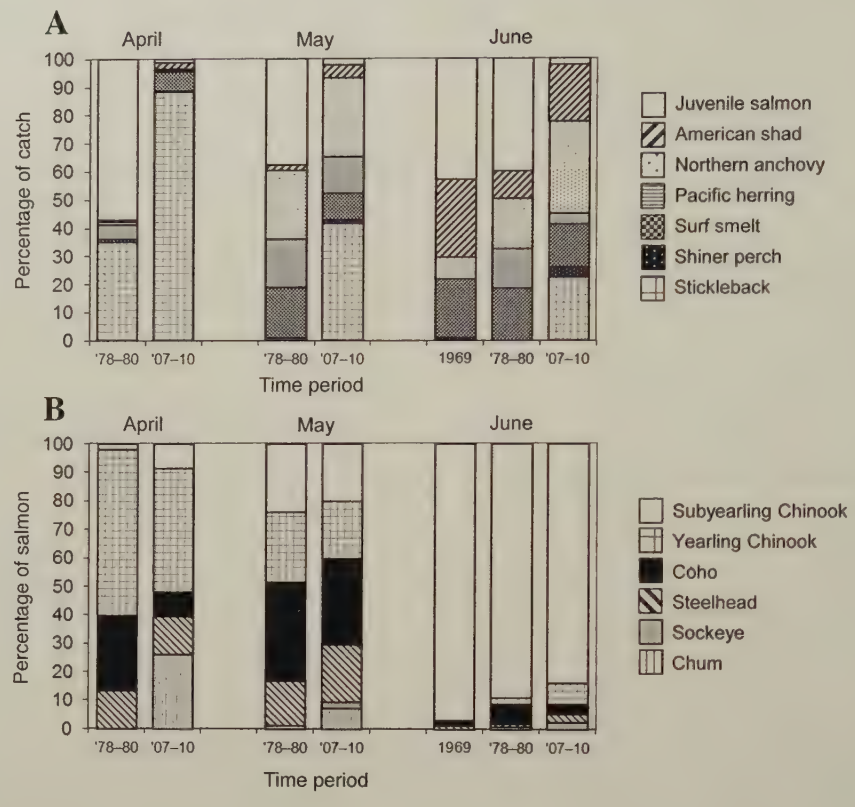

Figure 8

Comparison of purse seine catch data, summarized by month and time period from historical studies (1969, 1978–80) and our recent study (2007–10) of the fish assemblage in the lower Columbia River estuary. (**A**) Relative abundances of the dominant fish species—juvenile Pacific salmon (*Oncorhynchus* sp.; all species and age classes combined), American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), shiner perch (*Cymatogaster aggregata*), and threespine stickleback (*Gasterosteus aculeatus*). (**B**) Species-and-age composition of juvenile salmon, which comprises subyearling and yearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), sockeye salmon (*O. nerka*), and chum salmon (*O. keta*). Data sources for other two studies: for the year 1969—Johnsen and Sims, 1973; for the years 1978–80—Dawley et al.[7] Johnsen and Sims (1973) did not differentiate between subyearling and yearling (age 1) Chinook salmon; therefore, all fish of this species were assigned to the subyearling Chinook category.

April, but our observation may reflect changes in hatchery practices.

Recoveries of fish tagged with CWTs and PIT tags indicate that individuals originated from all accessible portions of the Columbia River, including the lower, mid-, and upper Columbia and Snake and Willamette rivers (Table 5)—an observation that also was made in an earlier study (Dawley et al.[2]). However, tagging effort is not consistent throughout the Columbia River (RMIS database; FPC database); therefore, the relative number of fish originating from different parts of the Columbia River provided in Table 5 reflects both fish origins and tagging effort. In the extreme case, we recovered steelhead with CWTs from only the upper Columbia and Snake rivers because those basins are the only areas where steelhead tagged with CWTs are released.

Perhaps most surprising was our estimate that most of the juvenile salmon that we caught were of hatchery origin (91–99%; Table 4), percentages that are considerably higher than the hatchery percentages reported for adults (34–80%; NRC, 1996; ISAB[1]). The percentages of clipped subyearling (76.0%; Table 4) and yearling (86.9%) Chinook salmon we observed were also higher than the percentages reported for juvenile subyearling and yearling Chinook salmon collected in nearby shal-

low water with a beach seine in 2007–08 (53.2% and 73.7%, respectively; Roegner et al., in press). This finding suggests that relatively more unclipped (presumably wild) Chinook salmon were closer to shore.

This overwhelming hatchery origin is consistent with the low variation we observed in the timing of juvenile salmon presence and abundance in the estuary (Fig. 4) and fish size (Fig. 6), given that most hatchery fish are released at a target size and date, with little variation from year to year (FPC database). Accordingly, we would expect to see greater variation in both timing and size of salmon if more fish were of wild origin, because of the greater fine-scale life history diversity observed in other wild-dominated systems and historically within the Columbia River (Rich, 1920; Myers and Horton, 1982; Burke, 2004, Bottom et al., 2005; Campbell, 2010).

For our calculation of the percentage of hatchery fish, we assumed that the survival of all hatchery fish migrating from the hatchery to the estuary is equal. However, this assumption is unlikely to be true because fish that travel longer distances and pass through more mainstem dams have greater mortality (Williams et al., 2001). This differential mortality undoubtedly contributed to the inflated percentages of hatchery subyearling Chinook and coho salmon we estimated (>100% in multiple years because percentages of clipped fish in our catches exceeded percentages of clipped fish reported at hatcheries). For these 2 groups, survival rates were likely to differ by distance from the estuary, and the percentage of clipped fish varied as well. The percentage of clipped subyearling Chinook and coho salmon released in the upper Columbia and Snake rivers were much lower (43–46% for subyearling Chinook, 7–36% for coho) than the percentage of fish released lower in the basin (90% for subyearling Chinook, 76% for coho). Although these releases in the upper basin are a small fraction (<29%) of the total releases every year, higher expected mortality rates would inflate our estimates of hatchery influence, likely contributing to our extremely high estimates for both species. Consequently, the percentage of clipped fish we observed in the estuary for these 2 species (76–77%, Table 4) represent the minimum hatchery influence; the true level of hatchery influence cannot be estimated without methods of assigning origin for unclipped fish (e.g., using scales, otoliths, or other means). This bias should not influence estimates for yearling Chinook salmon or steelhead, however, because mark rates are more consistent across the Columbia basin (FPC database). Clearly, clipping all hatchery fish would greatly increase our ability to identify hatchery fish and result in better estimates of hatchery influence and detection of potential ecological interactions.

We also observed that clipped (hatchery) coho salmon and steelhead were larger than their unclipped (hatchery and wild) counterparts. In stream environments, such size discrepancies have been shown to have negative consequences for wild fish (Weber and Fausch, 2005), although whether this finding applies to estuarine environments has not been addressed (Naish et al., 2008). Two recent studies in which juvenile (age 1.0) Chinook and coho salmon were examined in marine environments revealed no evidence for competitive advantage (in the form of feeding intensity or prey selection) of larger hatchery individuals over their unclipped (and smaller) counterparts (Sweeting and Beamish, 2009; Daly et al., 2011).

We did not observe a size difference between clipped and unclipped subyearling and yearling Chinook salmon. However, actual size variation between clipped and unclipped Chinook salmon may have been confounded by our length-based age assignment; small, unclipped yearling Chinook salmon may have been incorrectly assigned to the subyearling age category while large, clipped subyearling Chinook salmon may have been assigned to the yearling category. In addition, the size of Chinook smolts released from different hatcheries can vary greatly (FPC database), adding to the confusion. Restriction of such size comparisons to specific salmon stocks (e.g., Daly et al., 2011) would help resolve this issue.

Historical comparisons of fish communities in the lower Columbia River estuary

The fish assemblage we observed in 2007–10 generally was similar to that documented 3 or more decades earlier (Haertel and Osterberg, 1967; McCabe et al., 1983; Bottom and Jones, 1990). For example, all the species that we consistently caught (Tables 2, 3) were listed as commonly occurring in lower estuary pelagic habitats by earlier researchers (e.g., McCabe et al., 1983; Dawley et al.[7]; Bottom and Jones, 1990). As in these earlier studies, we did not catch any marine fish that might be predatory on juvenile salmon (e.g., adult lingcod, Pacific hake [*Merluccius productus*], and Pacific chub mackerel [*Scomber japonicus*]), with the exception of adult salmon. Haertel and Osterberg (1967) report that Pacific tomcod were a common species in their survey of estuarine fish in the 1960s (both juveniles and older fish), and Dawley et al.[7] report occasionally catching eulachon (*Thaleichthys pacificus*) and redtail surfperch (*Amphistichus rhodoterus*), neither of which we have encountered. Although the absence of eulachon in our catches is likely due to their recent population decline (Gustafson et al., 2011), the reason for the absence of other fishes is unknown.

The difference in abundance of American shad (which were primarily juveniles) in the estuary in 1978–80 and in 2007–10 (in our study) is consistent with changes in counts of adults across Bonneville Dam (FPS database). Specifically, data from Dawley et al.[7] indicates that American shad contributed 1%, 2%, and 10% to the fish assemblage in April, May, and June, respectively, in 1978–80, when dam counts averaged 947,000 adults. The relative abundance of American shad we observed in our study was roughly twice as high (2%, 5%, and 20% in April, May, and June, respectively), consistent with twice as many adults crossing Bonneville Dam

in 2007–10 (1.8 million; FPS database). By contrast, Johnsen and Sims (1973) report that in 1969, 27% of all fish caught were American shad, at a time when only 317,000 adults were counted crossing Bonneville Dam; the reason for this apparent discrepancy is unknown. Given the rapid expansion of American shad within the Columbia River (Hasselman et al., 2012a) and in marine waters along the west coast of North America (Pearcy and Fisher, 2011), there is increasing concern about the potential impacts of this exotic species on riverine, estuarine, and marine ecosystems (Pearcy and Fisher, 2011; Hasselman et al., 2012b).

As in our study, purse seines were used in 2 previous studies conducted in 1969 (Johnsen and Sims, 1973) and in 1978–80 (Dawley et al.[2, 7]) to sample the fish assemblage in open waters of the lower Columbia River estuary. However, these earlier studies used different-size nets (in length and depth but not mesh size) that were towed for 10 min before being closed. This methodological difference makes abundance comparisons among studies problematical, although we assume that species composition would be less affected (see discussion later in this section). These studies used the North Channel sampling location, eliminating possible site-specific differences. Comparison of the overall fish assemblage in the 3 time periods (1969, 1978–80, and 2007–10) indicates that the relative abundances of threespine stickleback and juvenile salmon are quite different between the earlier years and the most recent years (Fig. 8). Specifically, juvenile salmon in our study made up a small fraction (2%) of the overall catch, but historically they contributed between 43% and 57% of the total number of fish caught. In contrast, threespine stickleback were much more abundant in our study (averaging 88% of fish caught in April to 22% in June) than in earlier surveys (35% in April, <1% in either May or June) (Fig. 8A). Such changes in this estuarine fish community, if true, seem surprising at first glance but really are not unexpected given the substantial changes to fish assemblages documented farther upstream (Hughes et al., 2005; Maret and Mebane, 2005).

The relatively high proportion of juvenile salmon in estuarine catches in the late 1970s compared with that found in our study in 2007–10 could be a result of either lower juvenile salmon abundances, higher abundances of nonsalmon forage fish, or some combination of the two. Comparisons of hatchery production and total adult run size (hatchery and wild; size estimates for wild runs are not available basinwide) between the 2 time periods indicate that the latter—an increase in nonsalmon abundances—is largely responsible. For example, compared with the annual hatchery production levels (~140 million) in our survey years, hatchery production was similar (141 million) in 1969 and only moderately higher in 1978–80 (164–187 million) (Hilborn and Hare[8]). In addition, improvements to fish passage through mainstem dams have increased in-river survival (Williams et al., 2001), and, therefore, more juvenile salmon should currently survive downstream migration to the estuary than they did in earlier times. Similarly, a comparison of total (hatchery and wild) adult run sizes within the Columbia River between the 2 time periods indicates that total adult-run sizes were higher during our study than they were in the early 1980s. For example, annual counts of sockeye salmon and steelhead over Bonneville Dam in 1980–83 averaged 66,000 and 166,000 fish, respectively, but recent (2008–10) counts averaged 259,000 and 457,000 fish, respectively (FPC database). Similarly, estimated total in-river run size (which does not include catch in ocean fisheries that target fall [subyearling] Chinook and coho salmon) in 2008–10 for Chinook salmon (mean=843,000) and coho salmon (555,000) is higher now than in the early 1980s (556,000 Chinook and 294,000 coho salmon) (WDFW and ODFW[9]; PFMC, 2011). Assuming that predators, disease, and other sources of mortality are similar between the 2 time periods, these estimates of juvenile and adult abundances indicate that juvenile salmon should be as abundant—if not more so—in the Columbia River estuary during our study than they were 3 decades ago. This conclusion indicates that changes in the fish assemblage are most likely the result of increased abundance of nonsalmonids.

Methodological differences also may have contributed to these observed patterns because in the earlier studies the net was towed instead of being set in a circle as happens in round hauls. We examined whether this difference might influence catch composition by comparing the ratios of juvenile salmon or threespine stickleback to all fish caught in our round hauls (n=188) and tows (n=81) during cruises in which both were conducted. Although statistically significant differences were observed between tows and round hauls for the ratio of juvenile salmon to all fish (Bonferroni multiple comparison test, P<0.05), the differences were quite small (0.10 in round hauls, 0.12 in round hauls), and there were no statistically significant differences for the ratio of threespine stickleback to total catch between round hauls and tows (0.34 and 0.36, respectively). These results suggest that method of net deployment was unlikely to cause the observed differences. Although our abundance estimates are not directly comparable to the earlier data because of differences in techniques, our results certainly suggest that the abundance of nonsalmonids, especially of the threespine stickleback, has increased in recent years.

If these changes to the fish assemblage are indeed true, they likely reflect changes in environmental conditions in the Columbia River estuary. Over the last 150

[8] Hilborn, R, and S. R. Hare. 1992. Hatchery and wild fish production of anadromous salmon in the Columbia River basin. Fisheries Research Institute, Univ. Washington, Seattle, WA, Tech. Rep. FRI-UW-9207. [Available from http://www.fish.washington.edu.]

[9] WDFW and ODFW (Washington Department of Fish and Wildlife and Oregon Department of Fish and Wildlife ODFW). 2002. Status report: Columbia River fish runs and fisheries, 1938–2000, 324 p. [Available from WDFW, 600 Capitol Way N., Olympia, WA 98501-1091.]

years, major changes to the estuary have included decreased magnitude of the spring freshet, decreased salinity intrusion, and changes in estuarine bathymetry, the latter of which has influenced circulation patterns and habitat availability (Sherwood et al., 1990; Bottom et al., 2005). However, how environmental conditions have changed in the last 30 years has received relatively little attention (Bottom et al., 2006). It is known that spring river flow has been greatly reduced due to increased storage capacity of the hydrosystem. For example, average river flow in May and June measured at The Dalles Dam in 1977–81 was similar to recent (2007–10) levels; however, spring river flow in the 1960s and early 1970s was considerably greater (Bottom et al., 2006). Unfortunately, long-term salinity data are not available to determine how these flow declines may have influenced salinity intrusion. Limited temperature data from these earlier years suggest spring river temperatures were within the range presently observed (USGS National Water Information System).

It has been suggested that fish distributions in the Columbia River estuary are determined in part by prey availability (Bottom and Jones, 1990; Simenstad et al., 1990). If there was a time lag between declines in flow rates and a response by the fish assemblage (as might be expected if their prey are responding to flow rates), it may explain potential changes in the fish assemblage over the last 3 decades. Increasing numbers of forage fish also may explain the increasing abundance of avian predators in the Columbia River estuary, where these predators were largely absent 3 decades ago (Roby et al., 2003; Lyons, 2010). At present, we do not know whether changes in the fish assemblage have been beneficial or detrimental to juvenile salmon in the Columbia River estuary. Depressed populations of forage fish in Maine river basins are thought to inhibit the recovery of Atlantic salmon through a variety of ecological processes (Saunders et al., 2006). Whether similar ecological interactions between forage fish and Pacific salmon are occurring in the Columbia River basin is unknown.

Conclusions

We studied juvenile salmon and their associated fish community in open waters of the lower Columbia River estuary during spring in 4 years, 2007–10. During this period, we observed predictable seasonal changes in the abundance of all species of juvenile salmon, with low abundances in mid-April, peak abundances in May, and near absence by late June, except for subyearling Chinook salmon, which reached peak abundances in late June or early July. All caught juvenile salmon originated from throughout the Columbia River basin, and the vast majority (>90%) were of hatchery origin. Hatchery (i.e., clipped) steelhead and coho salmon were larger than individuals of the same species of unknown origin (unmarked hatchery and wild) but hatchery Chinook salmon were not, likely because of size overlap between large hatchery subyearling Chinook salmon and small wild yearling Chinook salmon. Although there was some variability in the abundance, timing, and size of juvenile salmon between years, no single year was exceptional with respect to these factors, as might be expected for fish with strong environmental influence. We hypothesize that the limited interannual variability we observed would have been higher if the proportion of wild fish also had been higher.

In contrast to highly predictable seasonal abundance of juvenile salmon, the abundance and species composition of the larger estuarine fish assemblage were extremely variable at temporal scales ranging from hours to years. This high variability is likely in response to extremely dynamic physical environments in the Columbia River estuary. Comparisons of our results with similar studies conducted over the previous 3 decades suggest major changes in the estuarine fish assemblage as a result of recent higher contributions of forage fish and threespine stickleback. The consequences of this change—whether it is beneficial or detrimental—to juvenile salmon is currently poorly understood. Although our research program has greatly increased our understanding of estuarine ecology in open waters of the Columbia River estuary in general and of juvenile salmon in these habitats in particular, there is clearly much that we do not know and hope to find out.

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Effect of sampling interval on estimates of larval supply

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Abstract—Estimates of larval supply can provide information on year-class strength that is useful for fisheries management. However, larval supply is difficult to monitor because long-term, high-frequency sampling is needed. The purpose of this study was to subsample an 11-year record of daily larval supply of blue crab (*Callinectes sapidus*) to determine the effect of sampling interval on variability in estimates of supply. The coefficient of variation in estimates of supply varied by 0.39 among years at a 2-day sampling interval and 0.84 at a 7-day sampling interval. For 8 of the 11 years, there was a significant correlation between mean daily larval supply and lagged fishery catch per trip (coefficient of correlation [r]=0.88). When these 8 years were subsampled, a 2-day sampling interval yielded a significant correlation with fishery data only 64.5% of the time and a 3-day sampling interval never yielded a significant correlation. Therefore, high-frequency sampling (daily or every other day) may be needed to characterize interannual variability in larval supply.

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Estimation of the supply of larval shellfishes and finfishes entering estuarine nursery habitats can provide important information on variability in year-class strength of many commercially important coastal species. The episodic nature of larval supply is a significant challenge to the generation of accurate estimates of larval supply (e.g., Dixon et al., 1999). Sampling must be conducted frequently enough to capture pulses in larval supply, but frequent sampling is costly and time consuming. Hettler et al. (1997) examined the effect of reduced sampling frequency by subsampling from a data set of daily supply of larval Atlantic menhaden (*Brevoortia tyrannus*) and determined that the variability of annual estimates of larval supply was "acceptable" [their term] on the basis of the standard error of estimates at sampling intervals of 7 days or less. Intervals of 14 and 30 days were deemed to be too long to be useful for estimation of annual larval abundance. Because their analysis was derived from a single year of data on daily larval supply, it did not account for interannual variations in the pattern of daily supply. In a long-term study of settlement of postlarvae (megalopae) (a proxy for larval supply) of blue crab (*Callinectes sapidus*), we observed a difference of 2 orders of magnitude in larval supply among years (Ogburn et al., 2012). This variability was due to changes in 1) the magnitude of daily larval supply, 2) the length of the larval settlement season, and 3) the number of pulses in settlement that occurred each year. Such interannual variability has the potential to strongly affect estimates of larval supply derived at a sampling interval of 7 days. The purpose of this study was to evaluate the effect of sampling at intervals of 1, 2, 3, 4, 5, and 7 days on the variability of estimates of annual larval supply derived from an 11-year record of blue crab megalopal settlement.

Adult blue crabs live in estuaries of the western Atlantic from Nova Scotia to Argentina. Mature females migrate to coastal areas where they release several clutches of larvae (Carr et al., 2005, Dickenson et al., 2006, Darnell et al., 2009). Planktonic larvae develop in 30–50 days in surface waters of the continental shelf (Costlow and Bookhout, 1959) and return to estuarine nursery habitats as megalopae (Orth and van Montfrans, 1987). The settlement of megalopae in estuaries is higher during nighttime flood tides than during daytime flood tides or during ebb tides (DeVries et al., 1994), but the annual pattern of larval settlement depends on the interaction between atmospheric forcing mechanisms and nighttime flood tides (Little and Epifanio, 1991; Ogburn et al., 2009).

Interannual variability in blue crab larval supply may be an important source of variability in annual fishery landings (Forward et al., 2004;

Ogburn et al., 2012). Therefore, estimates of larval supply could be a useful tool for fisheries managers; however, to aid management, monitoring must be cost effective and time efficient even as it is conducted in ways that minimize sampling error. The objectives of this study were to determine the variation in estimates of annual larval supply at sampling intervals of 1, 2, 3, 4, 5, and 7 days and to compare the utility of estimates of annual larval supply derived from these different sampling intervals for predicting fishery landings.

Materials and methods

Daily larval supply was determined through the collection of nightly megalopal settlement data at the dock of the Duke University Marine Laboratory in the Newport River estuary, North Carolina. Megalopae were sampled nightly with 3 replicate "hog's hair" settlement collectors during the period from September to November in each of 8 years from 1993 to 2003; data were not collected in 1997, 1999, or 2001 (Forward et al., 2004). In 2004–06, the other 3 years in our 11-year record, data were collected from June to November (Ogburn et al., 2009). Collectors were rinsed in freshwater to remove megalopae according to standard protocols (Metcalf et al., 1995), and megalopae were identified to genus by following Ogburn et al. (2011). Some megalopae may have been the lesser blue crab (*Callinectes similis*), but these megalopae likely made up <5% of the total number of megalopae collected (Ogburn et al., 2012). Detailed descriptions of the methods that we used in this study can be found in Forward et al. (2004) and Ogburn et al. (2009). Before analysis, gaps in settlement time series were filled by using linear interpolation. Differences in the variability of daily larval supply among years were explored through calculation of the mean number of megalopae collected in each hog's hair collector for each day (megalopae collector^{-1} day^{-1}), standard error of the mean, and index of dispersion (ID=variance/mean).

To generate estimates of annual larval supply at different sampling intervals, the daily supply data were subsampled at intervals of 2, 3, 4, 5, and 7 days because these intervals were the simulated sampling intervals used in Hettler et al. (1997). Subsampled time series were generated beginning with each possible start date such that there were 2 subsampled data sets at a 2-day interval beginning on either day 1 or day 2 of the original daily data, 3 data sets at a 3-day interval beginning on day 1, day 2, or day 3 of the original daily data, and so on. Mean daily settlement was used as the proxy for annual larval supply. For comparisons of interannual variability and sampling interval, we calculated the coefficient of variation (CV) of the annual means for the 11 years of data for each sampling interval.

Observed and subsampled estimates of annual larval supply were compared with data on fishery landings with correlation analysis. Data on fishery landings (in kilograms) and effort (catch per trip) were obtained from the North Carolina Division of Marine Fisheries for hard, soft, and peeler crabs landed statewide in the crab pot fishery. Catch per unit of effort (CPUE) was compared with mean annual larval supply derived from daily sampling at a lag of 2 years, the approximate age at which crabs enter the fishery (Forward et al., 2004). Confidence intervals were calculated as in Wing et al. (1995). CPUE data were not available for comparison with 2005 and 2006 larval supply at the time of this analysis. One outlier (1994 larval supply and 1996 landings) was removed before analysis because of extremely high CPUE relative to larval supply. The remaining estimates of mean annual larval supply were significantly correlated with CPUE (coefficient of correlation [r]=0.88, P=0.003). These estimates represent a useful sample data set derived from observed data for testing the effect of sampling interval on recruit–stock relationships. Please note that this analysis is not intended to be a recruit–stock analysis for the blue crab fishery in North Carolina. For such an analysis, see Ogburn et al. (2012).

Subsampling the data on daily larval supply generated more than one estimate of supply for each year, yielding many possible combinations of annual estimates. For example, there were 2 possible abundance estimates for each year at a 2-day sampling interval, depending on the start date of sampling (e.g., sampling start date of 1 September or 2 September). With 2 possible values for each of the 8 years of data, there were 2^8 or 256 possible data combinations. The number of possible combinations increased dramatically with sampling interval (Table 1). For the subsampled estimates of larval supply, significant correlations between lagged supply and CPUE were considered to be those correlations that exceeded the 95% confidence interval of the comparison between data from daily sampling and CPUE (r>0.69). Analyses were conducted in ActiveState Perl, vers. 5.10.0 (The Perl Foundation, Walnut Creek, CA[1]).

Results

The variability of estimates of annual larval supply was higher in years dominated by a single large pulse in larval supply and increased as sampling interval increased. For the sample period of September to November, both the ID (calculated from daily data; Fig. 1) and the variation in estimates of annual larval supply at the 2-day sampling interval (Fig. 2) were lowest in 1998 (ID=34; 10.8–11.1 megalopae collector^{-1} day^{-1}) and highest at the 7-day interval in 1996 (ID=2027; 29–167 megalopae collector^{-1} day^{-1}). The mean CV of the 7-day sampling interval was more than 2.5 times the mean CV of the 2-day interval (Table 2). Extending the sampling period to June–November (2004–06 only)

[1] Mention of trade names is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

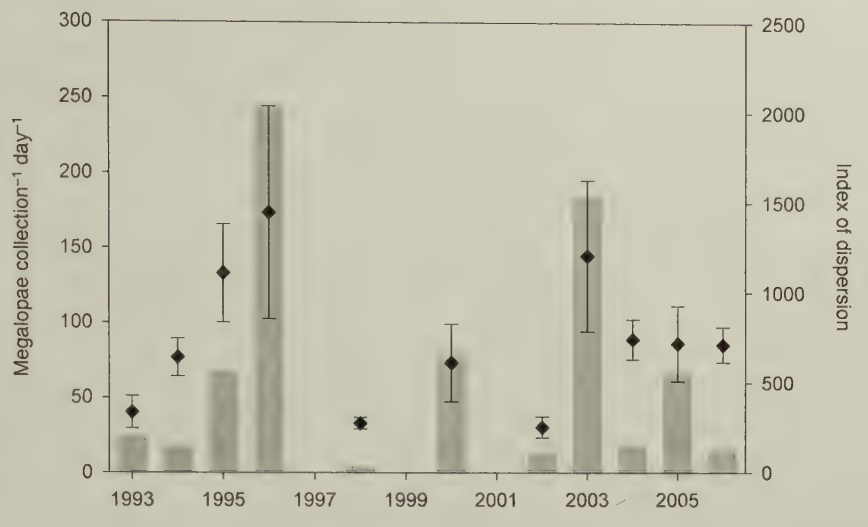

Figure 1

Variability of daily blue crab (*Callinectes sapidus*) larval supply, measured as number of megalopae collected in each hog's hair collector during each day (megalopae collector^{-1} day^{-1}) for each year of an 11-year record (1993–2006) used in this study to evaluate the effect of sampling at intervals of 2, 3, 4, 5, and 7 days on the variability of estimates of annual larval supply of blue crab megalopal settlement in the Newport River estuary, North Carolina. Data are the mean and standard error of the mean of larval supply (black diamonds and error bars) and the index of dispersion (gray vertical bars). No sampling was conducted and no data collected in 1997, 1999, and 2001.

resulted in a 20% decrease in the CV (from a mean of 0.27 to 0.22) at the 7-day interval (Table 2). The CV was typically small in years, such as 1998 (CV=0.34 at the 7-day interval), when supply was spread over many days (Fig. 3A) and large in years, such as 2000 (CV=0.99 at the 7-day interval), in which supply was dominated by a single pulse (Fig. 3B).

Subsampled estimates of annual larval supply were rarely correlated with CPUE of the crab fishery at sampling intervals >2 days. At a 2-day sampling interval, larval supply was significantly correlated with landings for 64.5% of possible comparisons (Table 1). There were no possible combinations of estimates of larval supply that were correlated with CPUE at the 3-day sampling interval. A small proportion of combinations (<15%) were significantly correlated with CPUE for longer sampling intervals, primarily because of an increase in the range of correlation coefficients with an increasing number of comparisons even as the mode decreased (Table 1).

Table 1

Sampling intervals, numbers of possible comparisons between annual estimates of blue crab (*Callinectes sapidus*) larval supply and catch per unit of effort in the North Carolina blue crab fishery (N), percentages of comparisons with significant correlations (type-1 error [α]=0.05 coefficient of correlation [r]>0.69), modes of correlation coefficients, and differences between the lowest and highest values of correlation coefficients in this study to evaluate the effect of sampling at intervals of 1–7 days on the variability of estimates of annual larval supply derived from an 11-year record of blue crab megalopal settlement.

Interval	N	% significant	Mode	Difference
1	1	100	0.88	—
2	256	64.5	0.68	0.30
3	6561	0	0.59	0.41
4	65,536	2.3	0.56	0.87
5	390,625	7.4	0.52	1.08
6	1,679,616	7.9	0.54	1.10
7	5,764,801	13.8	0.5	1.22

Discussion

Monitoring the supply of larval shellfishes and finfishes is a costly and time-consuming endeavor. Researchers often use sampling intervals of a week or more to reduce the cost and effort associated with data collection (e.g., Warlen, 1994), but it is important to fully understand the consequences of choosing a particular sampling interval. Sampling at intervals longer in duration than the wind or tide-driven processes that underlie fluctuations in larval supply could result in high variability in esti-

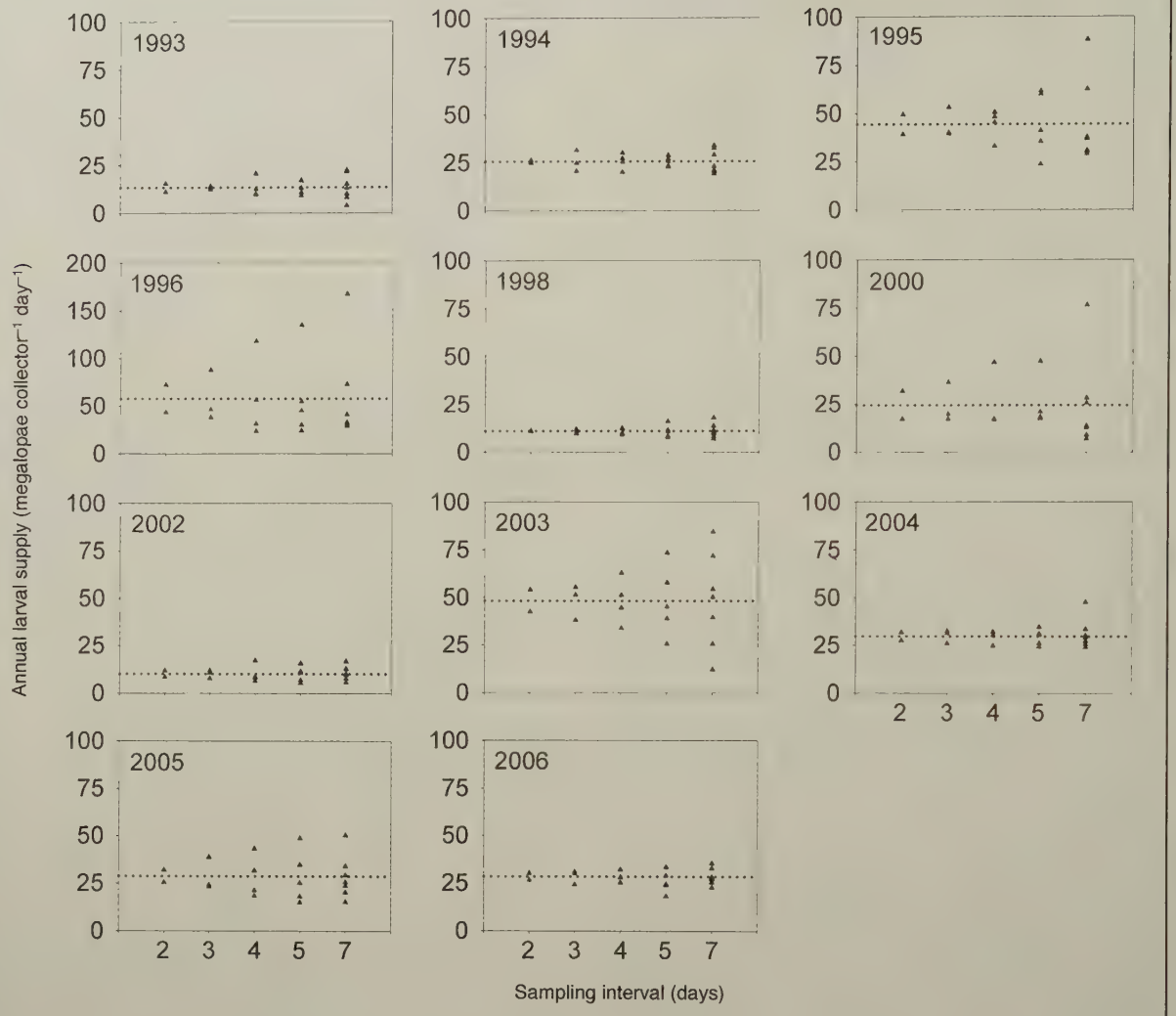

Figure 2

Estimated annual larval supply (megalopae collector^{-1} day^{-1}) of blue crab (*Callinectes sapidus*) megalopae at sampling intervals of 2, 3, 4, 5, and 7 days (triangles) compared with annual larval supply from daily sampling (dotted lines). Estimates were generated by subsampling data sets of daily larval supply for megalopae collected from September to November in each year of the 11-year record used in this study. Note that the *y*-axis values for 1996 are twice those for other years.

mates of annual supply. Hettler et al. (1997) suggested that a weekly (7-day) sampling interval was sufficient for estimating the annual supply of larval Atlantic menhaden in the Newport River estuary, North Carolina, but their analysis did not account for interannual variability in the pattern of larval supply because it was based on a single year of data. We detected large differences in the variability of daily larval supply among years, suggesting that a single year of daily data collection is insufficient to characterize variability in larval supply. We recognize that our study is not directly comparable to that of Hettler et al. (1997) because of differences in sampling gear (settlement collectors vs. plankton nets) and potential differences in the temporal dynamics of larval supply among species. Regardless of these factors, if Hettler et al. (1997) conducted their study in a year of unusually episodic larval supply, they may have overestimated variability in annual estimates of supply at each sampling interval. More important, if their study was conducted in a year in which larval supply was relatively constant over time, they may have dramatically underestimated variability.

The increase of the sampling interval from daily to every other day (2-day interval) decreased the chances of detecting a significant correlation between annual blue crab larval supply and CPUE in the North Carolina pot fishery to only 65% when a significant correlation (r=0.88) was observed for daily data. Significant correlations were never detected at a 3-day sampling interval but were detected at longer intervals, only

Table 2

Coefficients of variation for the September–November and June–November data sets on nightly blue crab (*Callinectes sapidus*) megalopa settlement. Data presented are for subsampling of the data sets of daily larval supply at intervals of 2, 3, 4, 5, and 7 days. Means and standard deviations (in parentheses) are included separately for the 2004–06 period for comparison between the September–November and June–November sampling periods; data were collected in the longer period from June to November only in 2004–06.

	Sampling interval				
Sept.–Nov.	2 days	3 days	4 days	5 days	7 days
1993	0.23	0.06	0.38	0.27	0.50
1994	0.04	0.21	0.16	0.10	0.24
1995	0.16	0.17	0.18	0.37	0.49
1996	0.35	0.45	0.75	0.77	0.88
1998	0.02	0.11	0.16	0.30	0.34
2000	0.43	0.43	0.61	0.54	0.99
2002	0.24	0.21	0.47	0.41	0.37
2003	0.17	0.19	0.25	0.38	0.52
2004	0.10	0.12	0.11	0.14	0.26
2005	0.16	0.30	0.39	0.48	0.40
2006	0.09	0.13	0.10	0.22	0.15
1993–2006 Mean	0.18 (0.13)	0.22 (0.13)	0.32 (0.22)	0.36 (0.19)	0.47 (0.26)
2004–06 Mean	0.12 (0.04)	0.18 (0.10)	0.20 (0.16)	0.28 (0.18)	0.27 (0.13)
June–Nov.	2 days	3 days	4 days	5 days	7 days
2004	0.03	0.14	0.04	0.05	0.20
2005	0.06	0.28	0.14	0.43	0.31
2006	0.04	0.01	0.06	0.06	0.14
2004–06 Mean	0.04 (0.02)	0.14 (0.14)	0.08 (0.06)	0.18 (0.22)	0.22 (0.09)

by chance as the range of correlation coefficients increased with an increasing number of possible data combinations (Table 1). This increase in the likelihood of detecting a significant recruit–stock relationship by chance at longer sampling intervals (nearly 14% at the 7-day interval) represents an additional concern for the design of larval-supply studies. Determining the level of variation that is appropriate for a particular sampling effort is not the subject of this article. However, if we set the maximum acceptable CV at 0.25, equivalent to 25% of the actual annual mean based on daily sampling, the 2-day sampling interval performed within this threshold in 9 of 11 years, but the 7-day interval provided a sufficient estimate of larval supply in only 2 of 11 years (Table 1). Assuming that extending the sampling period from 3 to 6 months would reduce the CV by 20% in all years, as observed in this study for 2004–06, we predicted there would have been no change in the number of years for which the CV exceeded 0.25. Therefore, scientists or managers must consider carefully the goals of multiyear larval surveys before they establish the appropriate sampling interval. For instance, weekly surveys probably are sufficient for estimation of seasonal trends in the supply, size, or age of larvae (Hettler et al., 1997). If the goal of a survey is to determine annual year-class strength, however, weekly sampling can result in widely ranging estimates of annual larval supply, and sampling daily or every other day may be necessary. It should be noted that we assumed that larvae do not remain on collectors for more than one day. Longer sampling intervals may be appropriate if larvae are retained on or in collectors for the entire sampling interval and if there are no density-dependent effects of additional larvae.

Conclusions

Determination of the acceptable level of variability in estimates of larval supply is the responsibility of the scientist or manager who is to conduct a particular survey. An increase in the sampling interval may reduce costs but can result in highly inaccurate estimates of abundance in some years. The episodic nature of blue crab larval supply appears to be consistent with other marine species (e.g., Warlen, 1994; Shanks and Roegner, 2007). Therefore, the results of this study are likely to apply across a wide range of marine species. If recruit–stock relationships are the goal of a larval-supply survey, we recommend that supply be sampled daily or every other day to maximize the likelihood of detection of significant relationships.

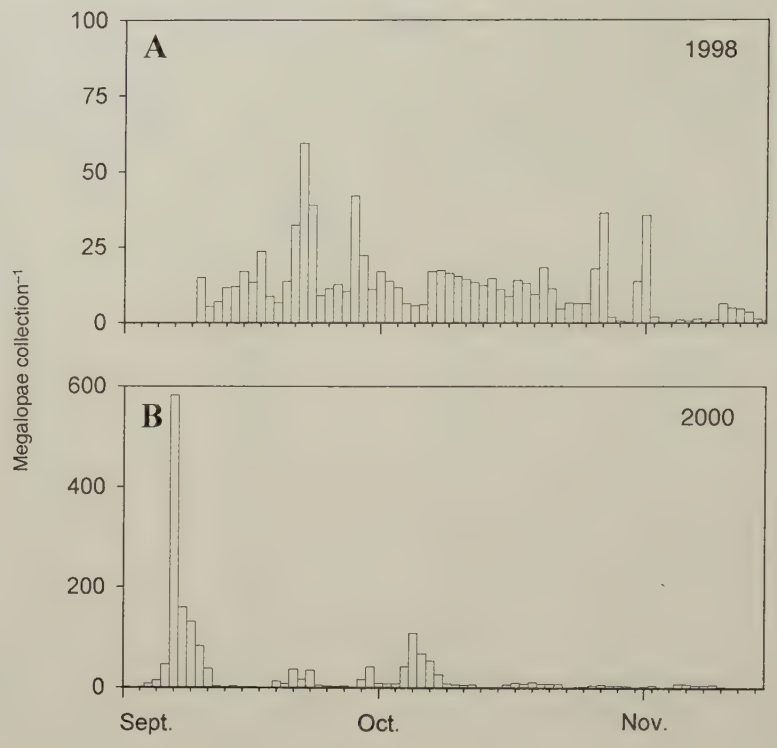

Figure 3

Daily larval supply (megalopae collector^{-1}) of blue crab (*Callinectes sapidus*) in (**A**) 1998, when larval supply was spread over several pulses, and (**B**) 2000, when most larval supply occurred in a single pulse.

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A comparison of size and age of red snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico

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Abstract—Despite extensive study, it still is not clear whether artificial reefs produce new fish biomass or whether they only attract various species and make them more vulnerable to fishing mortality. To further evaluate this question, the size and age of red snapper (*Lutjanus campechanus*) were sampled from April to November 2010 at artificial reefs south of Mobile Bay off the coast of Alabama and compared with the age of the artificial reef at the site of capture. Red snapper were collected with hook and line and a fish trap and visually counted during scuba-diver surveys. In the laboratory, all captured red snapper were weighed and measured, and the otoliths were removed for aging. The mean age of red snapper differed significantly across reefs of different ages, with older reefs having older fish. The mean age of red snapper at a particular reef was not related to reef depth or distance to other reefs. The positive correlation between the mean age of red snapper and the age of the reef where they were found supports the contention that artificial reefs in the northern Gulf of Mexico enhance production of red snapper. The presence of fish older than the reef indicates that red snapper are also attracted to artificial reefs.

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Red snapper (*Lutjanus campechanus*, Poey, 1860) has been historically targeted by both sport and commercial fishermen in the Gulf of Mexico (Camber, 1955). Because of intense fishing pressure, the estimated population abundance in this region has decreased and the stock is considered overfished (Schirripa and Legault, 1999; SEDAR[1]). Regulations that decrease the total allowable catch and shorten the recreational season have been enacted over the last several decades to reduce the harvest of this species and increase stock abundance.

The red snapper is a reef-associated fish that uses reef habitat as a resource for both shelter and prey (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; Piko and Szedlmayer, 2007; Gallaway et al., 2009). Age-0 red snapper begin to use reefs shortly after they settle out of the plankton and move to available low-relief, structured habitat (Workman and Foster, 1994; Szedlmayer and Howe, 1997; Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004). These new recruits quickly outgrow their initial benthic habitats and search for larger structured habitats by fall after the spawning season (Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004; Szedlmayer, 2011). After this initial recruitment, the presence of age-1 and older snapper, through predation and competitive exclusion, may limit the immigration of new recruits to reef structure (Bailey et al., 2001; Piko and Szedlmayer, 2007; Gallaway et al., 2009; Mudrak and Szedlmayer, 2012).

The substrate in the northern Gulf of Mexico is predominately mud and sand and has comparatively few natural reef areas (Parker et al., 1983; Kennicutt et al.,1995; Dufrene, 2005). The lack of naturally occurring reefs has stimulated the deployment of artificial reefs (e.g., decommissioned military tanks and concrete pyramids) by state agencies, private fishermen, and scientists to increase the availability of reef habitat. Several permit areas have been established off the coast of Alabama, where an estimated 15,000 artificial reefs have been deployed (Minton and Heath, 1998). The deployment of new reefs each year continues to add or replace reefs lost to major tropical storms.

The effect of artificial reefs on reef fish populations has been considered for decades. Bohnsack (1989) suggested that artificial reefs may simply aggregate fishes, making resident species easier to harvest and may ultimately decrease their populations. A second possibility is production enhancement, where reefs provide some limiting factor (e.g., habitat) that allows for an increase in the

[1] SEDAR (Southeast Data, Assessment, and Review). 2009. Stock assessment of red snapper in the Gulf of Mexico: SEDAR update assessment. Report of the update assessment workshop;, 24–28 August, 2009, 143 p. Miami, FL. NMFS, SEFSC, NOAA, Miami, Florida. [Available from http://www.sefsc.noaa.gov/sedar.]

available biomass of reef species. The artificial reef system in the northern Gulf of Mexico has been studied extensively— many studies focusing on various life history aspects of red snapper as a means to help resolve the question of whether or not artificial reefs enhance production.

The first group of studies involved diet analyses of the stomach contents of red snapper. If enhanced production is occurring, then red snapper diets should contain reef prey species; but, if only attraction is occurring, red snapper should be feeding on prey species not found on reefs. Evidence supporting both scenarios has been reported. For example, some studies reported that most red snapper prey items were species associated with the water column and sand-mud habitat (McCawley et al., 2006; Wells et al., 2008b). In contrast, other studies showed significant feeding on reef species (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; Redman and Szedlmayer, 2009).

Site fidelity of red snapper to artificial reefs also has been used to examine the question of enhanced production on artificial reefs. Again, 2 differing scenarios have been reported. Low residency and lack of site fidelity support the attraction hypothesis (Patterson et al., 2001b, Peabody, 2004), and long-term (>1020 d) residency on artificial reefs and high site fidelity support the production hypothesis (Szedlmayer and Shipp, 1994; Szedlmayer, 1997; Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping and Szedlmayer, 2011a; 2011b).

These previous studies indicate that attraction of red snapper to artificial reefs is occurring, but the extent to which artificial reefs also enhance production is an open question. Although it is relatively easy to provide evidence for attraction, it is not as easy to find evidence for production. Therefore, we contend that it still is not clear whether artificial reefs produce new red snapper biomass or whether they only attract fish of this species and make them more vulnerable to fishing mortality.

A new approach to this long-standing question would be to compare the age of resident fish with the age of the artificial reef where they occur. If enhanced production is occurring, new reefs should attract new recruits, and these recruits likely would stay and grow as their reef ages, becoming the dominate age class and would possibly exclude new recruits from the reef habitat. In this case, the age of fish resident at a reef should be positively correlated with the age of the reef. In contrast, if artificial reefs simply attract red snapper, reef age should not be correlated with fish age but, rather, should be related to the proximity of red snapper on other reefs and red snapper movement patterns. For our study, artificial reefs were deployed in 2006, 2009, and 2010, and the size and age of red snapper were compared among these 3 reef ages to help clarify whether artificial reefs may be enhancing red snapper production. The positions of these reefs were not released to the public to reduce the potential effects of variation in fishing mortality on age distributions of red snapper.

Figure 1

Map of sampling locations in our study of red snapper (*Lutjanus campechanus*) on artificial reefs in the northern Gulf of Mexico in 2010. Gray circles=reefs deployed in 2006; open circles=reefs deployed in 2009; and black circles=reefs deployed in 2010. Dotted lines indicate depth contours at 5-m intervals.

Materials and methods

Sample sites

The area of our study was located 20–30 km south of Mobile Bay, Alabama (Fig. 1). This area has more than 15,000 artificial reefs and a few natural, rocky reefs (Minton and Heath, 1998). For our study, artificial reefs (4.4×1.3×1.2 m, metal cages) were deployed in April 2006 (n=20, which became 4-year-old reefs in our study), April 2009 (n=10, which became 1-year-old reefs in our study), and January 2010 (n=10, which became 0.5-year-old reefs in our study). Reef locations were not published to limit potential fishing mortality. All the reefs we studied were located 1.3–1.7 km from other reefs deployed in this study. These reefs were deployed at the following depths: 27–32 m in 2006, 18–24 m in 2009, and 23–31 m in 2010.

All reefs were sampled from April to November 2010. The reefs deployed in 2010 were not sampled until at least 5 months after their deployment to allow adequate time for the immigration of red snapper (Mudrak and

Szedlmayer, 2012). Red snapper were collected with hook and line and fish trap from each reef. Hook-and-line sampling was standardized to 30 min and 2 individuals who fished. Fishing time was suspended when problems occurred (e.g., internally hooked fish) and continued once both individuals could resume fishing. For hook-and-line fishing, double 6/0 J hooks, 27.2-kg test monofilament line, 45.3-kg test monofilament leader were used, and whole Gulf menhaden (*Brevoortia patronus*) as bait. After completion of hook-and-line sampling, additional fish were collected with a baited fish trap (1.2×1.5×0.6 m; Collins, 1990). In the fish trap, both Gulf menhaden and whole squid (*Loligo* spp.) were used as bait. All fish traps were set for 15 min. After collections of red snapper reached ~50 individuals per reef, a diver released the number of fish caught above 50 fish by opening the trap door and allowing random individuals to escape at the surface—with one exception (73 red snapper were kept on 5 May 2010 because of the possibility of area closures that might have resulted from the Deepwater Horizon oil spill). When the minimum target of 30 individuals per reef was not reached after the first fish trap set, the trap was fished at least one additional time. All red snapper collected from a reef were immediately packed on ice and returned to the laboratory for further processing.

After fish collections were completed, 2 scuba divers completed visual counts and photographic (Nikon D200[2], Nikon Corp., Tokyo) and video (Sony CCD-TR101, Hi8, Sony Corp., Tokyo) recordings to use in estimation of the remaining red snapper at each sample site. A clear plastic jar containing cut Gulf menhaden was used to attract surrounding red snapper into aggregations during visual surveys for increased accuracy of total counts. Divers completed at least 3 full-circle point-and-count surveys, where the divers counted all fish within visual circular range, and the highest count was used for estimates of total abundance. Poor visibility at some sites limited these estimates. In addition, when sharks were present, diver operations were suspended, and visual estimates were completed later within 30 days of the original fish collections.

Laboratory analyses

Red snapper size (standard length [SL], fork length [FL], and total length [TL] in millimeters) and total body weight (0.1 g) were measured in the laboratory within 24 h of capture. For red snapper ≥250 mm TL, otoliths were removed with a Bosch fine-cut electric saw. For red snapper <250 mm TL, otoliths were removed with a small knife. Both left and right otoliths were removed from each fish, cleaned, and stored in dry plastic vials for later analysis. Opaque bands were counted on all otoliths for age estimates. For fish <7 years old, bands were counted on whole otoliths that were immersed in water and viewed under a dissecting scope with transmitted light. If ages were ≥7 years, thin otolith sections were prepared and bands were counted at 40× magnification with a compound microscope (Szedlmayer and Beyer, 2011). Opaque bands of sectioned otoliths were counted along the dorsal edge of the sulcus acousticus. Bands on each otolith were counted independently 4 times. After 4 readings, 2 readers examined the remaining otoliths for which counts still differed and attempted to reach a consensus on age. If an agreement on age could not be reached for an otolith, it was rejected. A reference collection of hatchery red snapper that had been released in the wild as age-0 and recaptured as age-1fish (n=22) along with a group that had been reared in captivity to age-1 (n=13) were used to validate counting methods of wild caught age-1 fish. Some of the otoliths of these known age-1 fish showed a "false" annulus (i.e., had 2 opaque bands) but showed age-1 otolith shape patterns (Beyer and Szedlmayer, 2010). Therefore, some of the wild fish <200 mm SL caught in this study that had 2 opaque bands were defined as age-1, on the basis of their age-1 shape patterns appearing similar to the shape patterns of hatchery-reared fish as well as hatchery-born but wild-reared fish.

Video recordings and digital photographs of the studied reefs were examined in the laboratory for comparisons and validation of the divers' visual counts. In the laboratory, photographs that showed the highest number of red snapper for a particular reef were selected for computer-based counting. All red snapper in these photographs were identified and counted through image analysis with Image-Pro Plus software (vers. 4.5, Media Cybernetics, Rockville, MD). Two screens were used to count fish in video recordings. A single frame captured from the video was displayed on one screen while the video played on the second screen. Because image quality decreases when a single frame of video is captured, we used the full video on the second screen to identify all the fish in the captured frame on the first screen. The captured video image then was marked and the fish in it were counted with Image-Pro software.

Data analyses

Catch per unit of effort (CPUE) for each reef was calculated for both hook and line (CPUE=number caught by 2 individuals/30 min) and trap (CPUE=number caught/15 min). The precision of age estimates between readers was compared with linear regression and average percent error (Beamish and Fournier, 1981). Densities of red snapper were estimated by adding the total number of red snapper caught (from both hook and line and fish trap) to the number of fish counted in the visual survey. Pearson's correlation coefficient was used to compare densities (number of fish per cubic meter of reef surveyed) among reefs of different ages, with reef age determined by the number of months that a reef had been deployed before the month of sampling. Analysis of variance (ANOVA) was used to compare the SL, weights,

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

and ages of red snapper among the different ages of reefs. If significant differences were detected, a Tukey test was used to show specific differences.

Growth rates were examined with an analysis of covariance (ANCOVA) that compared the mean length at age of red snapper <10 years old between old (2006) and new (2009 and 2010) reefs. This analysis was used to determine if old reefs were providing additional resources, a difference that would be reflected in faster growth rates of red snapper on old reefs than on new reefs. For additional comparisons, Pearson's correlation coefficients were calculated for reef age with red snapper SL, weight, and age. Also examined with Pearson's correlation coefficient was the potential influence of nearby known reefs on the age and abundance of red snapper on the reefs that we surveyed in 2010. Nearby reefs were 0.17–1.7 km away (mean=0.72 km, n=37), or less than the distance between the reef sites sampled in our study. In an effort to remove possible depth effects, the ages of red snapper collected at the same depth (30 m) were compared between the 2006 and 2010 reefs with a t-test. Differences were considered significant at $P \leq 0.05$, and all data were analyzed with Statistical Analysis System software (SAS, vers. 9.1, SAS Institute, Inc., Cary, NC).

Results

Red snapper were sampled from April to November 2010 from 37 artificial reefs (2006 reefs=18; 2009 reefs=10; 2010 reefs=9). Visual surveys were completed by divers at later dates at 2 sites because of the presence of sharks on the original sampling date and were not completed on 7 reefs (3 of the 2006 reefs and 4 of the 2010 reefs) because of poor visibility (<1 m).

A total of 1028 red snapper were collected, 439 by hook and line and 589 by trap. Mean ±standard deviation (SD) CPUE for hook and line was significantly greater on the 2006 reefs (20.4 ±8.5 30 min^{-1}) than on the 2009 (6.3 ±8.1 30 min^{-1}) and 2010 reefs (2.6 ±4.6 30 min^{-1}; ANOVA: $F_{2, 34}$=20.38, P<0.0001). No significant differences in CPUE were detected among reef years for trap collections (2006=10.6 ±10.9, 2009=16.6 ±19.9, and 2010=14.3 ±12.7; ANOVA: $F_{2, 34}$=0.6, P=0.55). The SL and weight of red snapper caught by hook and line (429.4 ±79.8 mm, 2531 ±1409 g) were significantly greater than those measures of fish caught by trap (232.6 ±77.6 mm, 538 ±726 g; SL t-test, t_{1018}=39.56, weight t_{1018}=29.41, P<0.0001). Red snapper ages also were significantly different between these 2 sampling methods (hook and line=4.1 ±1.3 years, trap=1.9 ±1.1 years; t-test, t_{1024}=29.68, P<0.0001).

The visual survey methods significantly affected counts of red snapper. Visual counts by divers (mean ±SD=78.3 ±54.8) were significantly higher than counts from image-analysis methods (photograph counts=30.7 ±20.2, video counts=16.5 ±10.3; ANOVA, $F_{2, 42}$=13.37, P<0.0001). Because of these differences, total densities of red snapper were estimated by adding the number of captured fish (hook-and-line and trap samples) to divers' visual counts.

Table 1

Average percent error for both sets of independent readings of otoliths from red snapper (*Lutjanus campechanus*) caught in 2010 during our study on artificial reefs in the northern Gulf of Mexico. Included are the percentages of agreement for each difference between readings (first and second reading, coefficient of regression [r^2]=0.83, P<0.0001; third and fourth reading, r^2=0.96, P<0.0001).

	First and second readings	Third and fourth Readings
Average percent error	7.85	1.41
Standard deviation	0.12	0.05
0	62.16%	92.32%
±1	35.89%	7.39%
±2	1.95%	0.29%
≥3	0%	0%

Age-1 red snapper composed the dominate age class on the 2010 reefs and recruited to these reefs in the early summer. Mean ±SD numbers of red snapper per cubic meter of reef structure increased as reef age increased (Pearson's correlation coefficient [r]=0.48, P=0.008) and were significantly greater on 2006 reefs (22 ±13) than on 2009 reefs (12 ±6) and 2010 reefs (8 ±7; ANOVA, $F_{2, 27}$=4.25, P<0.025).

All caught red snapper (n=1028: 2006 reefs=587, 2009 reefs=280, 2010 reefs=161) were used in the final age comparisons. Initial agreement between the first and second independent readings was 62.2% (639/1028). A third and fourth reading increased the accepted otoliths to 92.3% (949/1028). Average percent error was calculated for both sets of independent readings (Table 1). An age consensus was reached on all remaining otoliths (n=79) through simultaneous examination by the 2 readers. The reference collection of age-1 hatchery (n=35, laboratory and wild reared) red snapper showed 25.7% with 2 opaque bands, indicating that counting opaque bands for age-1 fish may not be reliable. Among fish that were <200 mm SL and showed 2 opaque bands (n=72), all were identified as age-1 based on shape, thickness, and location of the opaque bands (Beyer and Szedlmayer, 2010; Szedlmayer and Beyer, 2011).

Mean ±SD red snapper SL, weight, and age were significantly different among 2006 reefs (373.3 ±107.8 mm SL, 1883 ±1388 g, 3.5 ±1.2 years), 2009 reefs (250.2 ±114.7 mm SL, 852 ±1464 g, 2.0 ±1.7 years) and 2010 reefs (222.3 ±78.0 mm SL, 480 ±711 g, 1.7 ±1.0 years; ANOVA, $F_{2, 1025}$=194.2, P<0.0001; Table 2; Figs. 2 and 3). Reef age was positively correlated with red snapper age (Pearson's r=0.61, P<0.0001), standard length (r=0.71, P<0.0001), and weight (r=0.47, P=0.0035). Comparisons of linear growth rates for fish <10 years old showed no significant differences between old (2006)

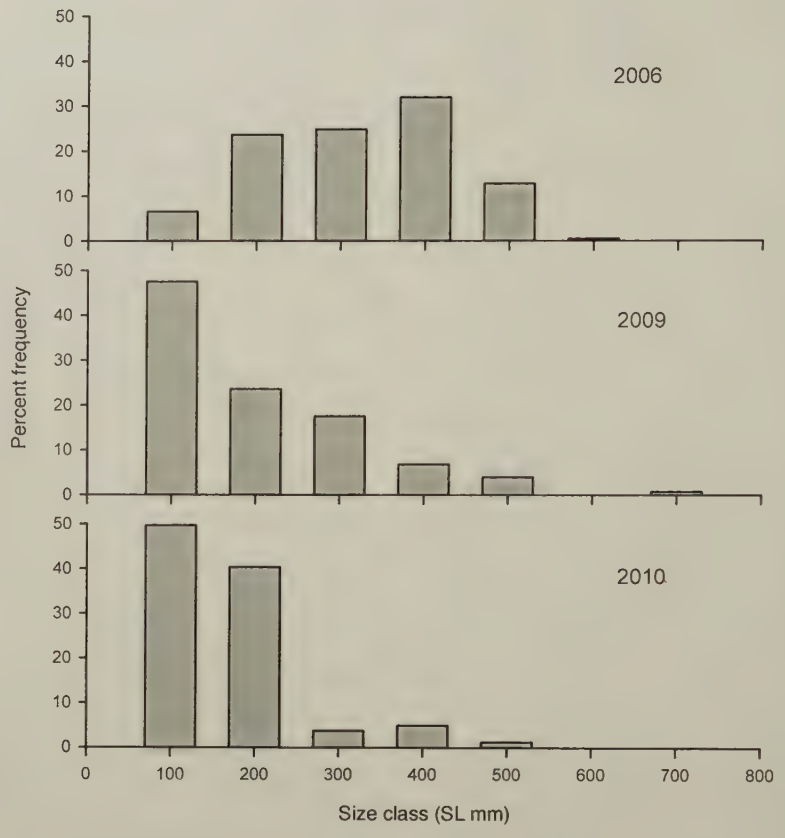

Figure 2

Length frequency of red snapper (*Lutjanus campechanus*) caught in our study on artificial reefs in the northern Gulf of Mexico in 2010, shown by year that reef was deployed, separated into 100-mm standard-length (SL) size classes (e.g., 100=100–199 mm).

Table 2

Mean (±SD) standard length (SL), weight, and age of red snapper (*Lutjanus campechanus*) caught during our study on artificial reefs deployed in 2006, 2009, and 2010 in the northern Gulf of Mexico. Superscript letters are used to indicate significant differences ($P \leq 0.05$). Included for each reef year are the total number of red snapper caught by hook-and-line and trap, mean diver count, and mean density estimate. Estimates of mean density per reef combine diver counts and catch of hook-and-line and trap.

Reef year	SL (mm)	Weight (kg)	Age (yr)	Hook and line	Trap	Diver count	Density
2006	373.3 ±107.8 ^{a}	1.88 ±1.39 ^{a}	3.54 ±1.24 ^{a}	20.2 ±8.8	12.4 ±11.3	115.5 ±87.8	148.7 ±92.5
2009	250.2 ±114.7 ^{b}	0.85 ±1.46 ^{b}	1.98 ±1.70 ^{b}	5.3 ±6.1	22.5 ±18.4	54.0 ±35.8	81.8 ±41.2
2010	222.3 ±78.0 ^{c}	0.48 ±0.71 ^{c}	1.72 ±1.00 ^{c}	2.3 ±4.6	15.6 ±11.6	36.0 ±31.7	55.6 ±45.6

and new (2009 and 2010) reefs (ANCOVA, $F_{3,\ 1018}$=2.98, P=0.085, power>0.99).

The mean depth (30 m) of the 2006 reefs were significantly greater than the mean depth (20 m) of the 2009 reefs (t-test, t_{26}=16.32, P<0.0001). Because of this depth difference, red snapper also were compared among the 2006 and 2010 reefs (n=8) with the same depth (30 m). These comparisons also showed significantly larger and older red snapper on the 2006 reefs (mean ±SD=368.7 ±5.0 mm SL, 1821 ±1326 g, 3.60 ±1.20 years) compared to 2010 reefs (236.2 ±85.2 mm SL, 578 ±814 g, 1.91 ±1.10 years; t-test, P<0.0001).

Comparisons of our estimates of red snapper abundance and age on artificial reefs by proximity (<1.7 km) to other known reefs not sampled in our study failed to detect a significant effect. These other nearby reefs have published locations because they are part of Alabama's artificial reef program and were deployed

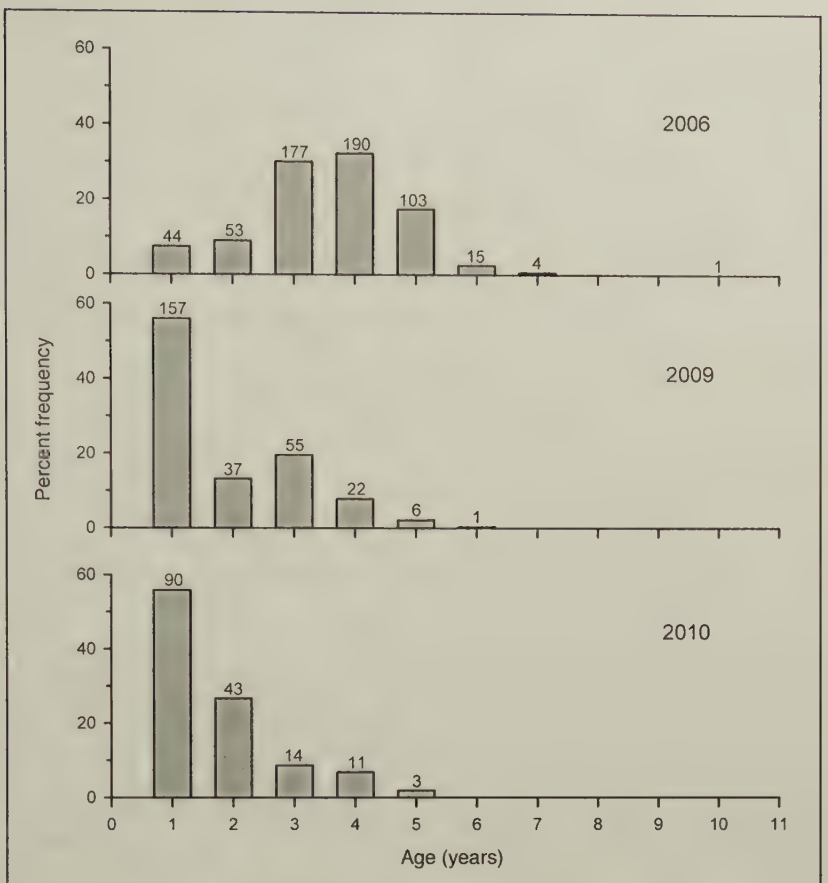

Figure 3

Age frequency, by year that reef was deployed, of red snapper (*Lutjanus campechanus*) caught in our study on artificial reefs in the northern Gulf of Mexico in 2010. Numbers above bars indicate total number of fish caught for each age class.

from 1992 to 2007. The oldest reef (1992) was closest to a 2010 reef that we sampled, and many of the artificial reefs deployed in 2004 and 2007 were within 1.7 km of reefs in all 3 reef ages that we sampled in our study (Fig. 4). No significant correlations were detected between distance to other reefs and abundance (Pearson's r=–0.045, P=0.781), or mean age of red snapper (Pearson's r=0.026, P=0.88; Fig. 5).

Discussion

Evidence for production and attraction

Our study showed that older red snapper were associated with older artificial reefs. Previous studies have compared artificial reef age with estimates of density and size of resident reef fishes but have not examined reef fish age. For example, densities of reef fishes and larger sparids (*Diplodus sargus*, *Diplodus bellottii*, and *Diplodus vulgaris*) have been reported to be significantly higher at older habitats (Lindberg et al., 2006; Santos et al., 2011). Because length varies directly with age with these species up to the age of 3 years (Gordoa and Molí, 1997), it is likely that their age also increased with reef age as was observed with red snapper in our study.

The relation between reef age and fish age shown in our own and these other studies, along with the long-term residence of red snapper on artificial reefs shown in previous studies (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer, 2011a), supports the hypothesis that artificial reefs enhance the production of red snapper (Szedlmayer and Shipp, 1994; Szedlmayer, 2007; Gallaway et al., 2009). If artificial reefs enhance a population and experience no fishing pressure, Powers et al. (2003) estimated that such reefs could increase production by 6.45 kg wet weight/10 m^2 in the first year after their deployment. Because the locations of the reefs in our study were not published, fishing mortality was limited and therefore had the potential to increase production.

It was also clear that attraction of fish plays an important role in the function of these artificial reefs. For example, fish older than the age of the reef were

present on the reefs that we sampled, including 2 of the oldest fish (19 and 14 years old) that were caught on the 2009 reefs. It is possible that larger, older red snapper become less dependent on particular reefs because of relief from predation pressure and may show greater movement among reef sites as they search for new prey resources (including young red snapper) on newly established reefs (Mudrak and Szedlmayer, 2012). However, although attraction is clear and accounts for both the initial recruitment of young fish and the presence of older red snapper, if attraction was the only function of artificial reefs, we would not expect a positive correlation between mean fish age and reef age. Instead, the age distribution of red snapper should be random or related to the proximity of nearby reefs. Hence, this study provides evidence that both attraction and production are important ecological functions of artificial reefs for red snapper populations in the northern Gulf of Mexico.

According to our study and several other studies, young fish (age-0 and age-1) will recruit to new habitat, usually small (1–7 m^3) artificial reefs (Gallaway et al., 2009; Szedlmayer, 2011; Mudrak and Szedlmayer, 2012). Many of these red snapper remain at such habitats for extended periods (up to several years; Szedlmayer,1997; Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping and Szedlmayer, 2011a, 2011b) and then begin to show greater movement as they become older and larger and are less vulnerable to predation (Gallaway et al., 2009). For example, on the basis of a 72% residency rate per year from telemetry studies (Topping and Szedlmayer, 2011a), and a mean of 45 age-1 recruits to new (1-year-old) reefs in our study, there would be ~18 age-5 red snapper per reef after 4 years. These estimates are similar to counts recorded for the 2006 reefs in our study, with a mean of 26 age-5 fish per reef (on the basis of proportions of age-5 red snapper among all fish captured from 2006 reefs, extrapolated to mean total densities on 2006 reefs). Also, these residency estimates based on telemetry are underestimates because the time that red snapper reside on a particular reef before being tagged is not included (Topping and Szedlmayer, 2011a). Laboratory and field studies indicate that these older age-5 red snapper may then competitively exclude and even cannibalize new recruits (Bailey et al., 2001; Piko and Szedlmayer, 2007; Mudrak and Szedlmayer, 2012), and perhaps contribute to the association between fish age and reef age. However, attraction may continue to play an important role as older fish that are better able to fend off aggression and cannibalism move to favorable habitats that still harbor abundant prey resources (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004).

Several studies suggest that red snapper populations have been overfished and that habitat limitation was not the most important controlling factor that contributed to declines in abundance (Schirripa and Legault, 1999; Patterson et al., 2001b; Cowan et al., 2011). Clearly, there was significant fishing mortality of red snapper in the northern Gulf of Mexico (Gillig et al., 2000). However, if fishing mortality was the only limiting factor for red snapper and habitat was not important, we would not expect reef age to have significant effects on fish age (i.e., all reefs, whether fished or not, would show similar age distributions). Red snapper enter the fishery at around age 2 (minimum size: recreational=406 mm TL, commercial=330 mm TL), and the catch consists predominately of 2- to 4-year-old fish. These ages represented 59% (n=602) of the total catch in our study and indicate that fishing mortality was not limiting red snapper abundance on the reefs investigated in our study.

One substantial difference between our study, which suggests habitat limitation, and previous studies, which

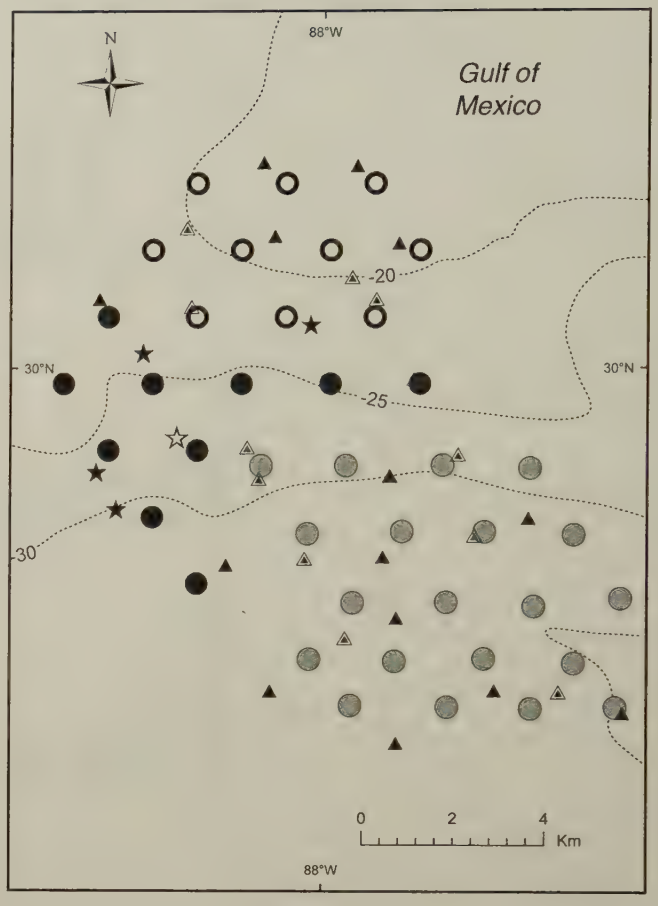

Figure 4

Map showing proximity of publicly known reefs to reefs sampled in 2010 in our study of red snapper (*Lutjanus campechanus*) on artificial reefs in the northern Gulf of Mexico. Note that the positions of the reefs sampled in our study were not released to the public. Study reefs: gray circles=reefs deployed in 2006; open circles=reefs deployed in 2009; and black circles=reefs deployed in 2010. Publicly known reefs: black stars=reefs of army tanks deployed in 1994–1995; black triangles=reefs made of concrete pyramids deployed in 2007; black and white triangles=pyramid reefs deployed in 2004; open star=barge deployed as a reef in 1994. Dotted lines indicate depth contours at 5-m intervals.

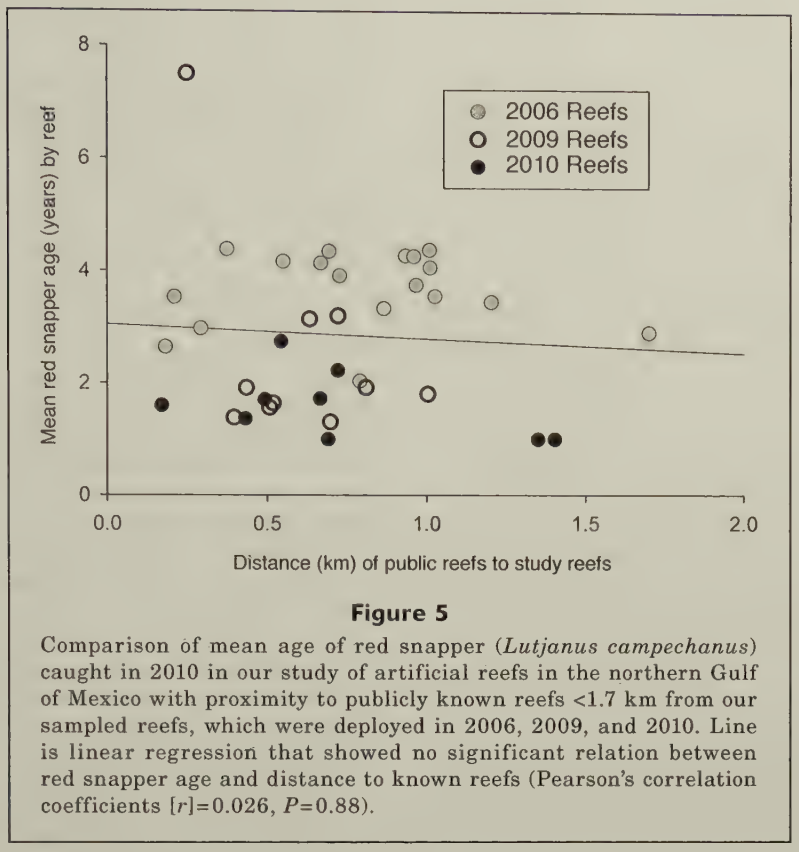

Figure 5

Comparison of mean age of red snapper (*Lutjanus campechanus*) caught in 2010 in our study of artificial reefs in the northern Gulf of Mexico with proximity to publicly known reefs <1.7 km from our sampled reefs, which were deployed in 2006, 2009, and 2010. Line is linear regression that showed no significant relation between red snapper age and distance to known reefs (Pearson's correlation coefficients [r]=0.026, P=0.88).

suggested fishing mortality limitation, was the use of fishery-independent data rather than fishery-dependent data. Although other studies used mainly fishery-dependent data on red snapper caught by sport and commercial fishermen (Szedlmayer and Shipp, 1994; Baker and Wilson, 2001; Patterson et al., 2001a; Wilson and Nieland, 2001), we used fishery-independent methods at unpublished artificial reef sites. These fishery-independent methods also allowed us to sample red snapper that were too small to be counted with fishery-dependent methods. In addition, fishing mortality at reef sites surveyed in our study was probably far more reduced than at known reefs because the locations of the artificial reefs that we sampled were unpublished and likely had limited access for fishing.

Several alternative factors, aside from reef age, could have affected the size and age of red snapper caught on the artificial reefs examined in our study. Additional prey may be one important factor that created differences in habitat value among reefs of different ages, and these differences may have resulted in larger, older fish at older reefs. If older reefs were providing more prey resources, we would expect that red snapper on these reefs would have higher growth rates, especially the relatively young (<10-year-old) individuals that have a nearly linear growth rate. Yet no significant differences in mean growth rates of red snapper were detected among the reefs sampled, despite their age differences. Even so, older reefs often have more well-developed epifaunal benthic communities that can influence habitat value (Redman and Szedlmayer, 2009), and this development might be expected for older artificial reefs like those in our study. If older reefs actually provide more prey resources or greater habitat complexity and shelter than younger reefs, attraction to these "better" reefs may account for some of the older ages and higher abundances of red snapper on older reefs. However, we still are left with the same conclusion: artificial reefs enhance red snapper production. One implication of our study is that habitat value may vary not only spatially (e.g., open versus structured habitats) but also temporally (e.g., new versus older, more "developed" reefs). Therefore, we need to include a temporal component to habitat value, whereby new artificial reefs may need time to develop before they start to enhance production.

Another factor that may have caused differences in the ages of fish among reefs was reef depth. The mean depth of the 2006 reefs was 30 m, but the mean depth of the 2009 reefs was 20 m, and there is some evidence that larger, older red snapper were more common in deeper offshore waters than in shallower nearshore waters (Render, 1995; Mitchell et al., 2004). However, comparisons of reefs with the same mean depth (30 m) and distance from shore (27 km) still showed significantly larger and older red snapper at the 2006 reefs than at the 2010 reefs. In addition, the distances among the reefs that were farthest apart were relatively smaller (14 km) than the distance across the continental shelf (110 km) where depth-related differences in size and age may be more apparent (Mitchell et al., 2004).

We also considered the possible emigration of larger, older red snapper from other reef sites or an effect of nearby reefs not sampled in our study. Proximity to other natural or artificial reefs has been shown in other studies to be an important factor that can affect density of reef fishes (Jessee et al., 1985; Sogard, 1989; Strelcheck et al., 2005; Shipley and Cowan, 2010). In our study, no significant relations were detected between proximity of our study reefs to other reefs and red snapper ages or abundance. In general, other artificial reefs were, for the most part, evenly distributed across our overall study area (Fig. 1) and would not be expected to bias red snapper age distribution to either younger or older reef sites in our study (Fig. 4).

Comparison of collection methods

This study supports previous studies on the importance of using several collection methods to adequately estimate size and age distribution of red snapper on artificial reefs (Myers and Hoenig, 1997; McClanahan and Mangi, 2004; Szedlmayer, 2007; Wells et al., 2008a; Gallaway et al., 2009). Hook-and-line and fish-trap methods are known to be size selective, and red snapper caught in our study were consistently larger with hook-and-line than with fish traps. This difference occurred mostly because larger fish are able to swallow whole bait and smaller fish consume smaller portions. In addition, smaller fish are more likely to enter a trap, and larger fish may be limited by the size of a trap opening. The distinct size differences observed in our study also could have been influenced by differences in bait: the fish traps had squid in addition to Gulf menhaden, but the hook-and-line bait was strictly Gulf menhaden.

The divers' visual counts were used to estimate the red snapper remaining present on the reef after hook-and-line and trap sampling. At 2 sample sites, visual surveys were conducted a maximum of 30 days after our initial sampling because sharks were present during our initial sampling. Although it is possible that additional red snapper immigrated to the reef at these 2 sites within that 30-d time period, it is unlikely that enough fish recruited to cause a bias in our abundance estimates. This notion is supported by evidence from telemetry studies of high site fidelity for red snapper (72% residency rate per year; Topping and Szedlmayer 2011a) and by the fact that diver counts typically underestimate abundance. In comparison with results from visual surveys, counts were significantly lower from the video and photographic methods. These differences mostly were due to fish swimming throughout the part of the water column that was not within the field of view of the cameras. A bait jar was used with the intent to attract fish closer to the cameras and reduce these differences, but it had only limited success. Comparisons of counts from remote, underwater, baited cameras with those from scuba-diver surveys have shown similar results, with diver visual surveys showing the greatest abundance and diversity of fishes among the methods compared (Tessier et al., 2005; Langlois et al., 2006). Because counts from photographs and video recordings were lower, we used the divers' counts in our estimates of red snapper density for each reef. However, the photographs and video recordings were still important in verifying species identification.

Artificial reef succession and red snapper densities

The reefs in our study supported higher densities of red snapper than reefs sampled in previous studies. In a demolition study of 9 offshore oil platforms, mean density of red snapper was 0.24 individuals/m^3 (Gitschlag et al.[3]). In another study of platforms where stationary hydroacoustics and visual diver counts were used, mean density was 0.16 individuals/m^3 (Stanley and Wilson, 1997). Substantially higher than these platform estimates, the estimates from our study of total density of red snapper were 1.6–47.9 individuals/m^3, with a mean of 15.7 individuals/m^3. One difference between our study and these previous studies was the larger size of the platforms surveyed which also encompassed the entire water column. The volume of these platforms varied: 1037–29,860 m^3 (Gitschlag et al.[3]) and 19,800 m^3 (Stanley and Wilson, 1997); in contrast, all reefs in our study had a volume of 6.9 m^3. However, even if the volume estimates of these platforms were reduced by two-thirds (to account for the habitat in the upper water column that red snapper typically do not use), mean densities of red snapper on platforms would be 0.73 individuals/m^3 (Gitschlag et al., 2000[3]) and 0.47 individuals/m^3 (Stanley and Wilson, 1997)—levels that would still be considerably less than the estimates from our study of artificial reefs formed from metal cages.

These differences in the density of red snapper among artificial habitats may be due to higher habitat complexity and associated enhanced protection from predation, additional prey resources, and fewer resident larger predators at cage reefs than at platforms. The densities of lemon damselfish (*Pomacentrus moluccensis*) found on highly complex coral reefs with predators were similar to densities found on reefs where predators were excluded, indicating that these complex coral habitats provided protection for this species (Beukers and Jones, 1997). Similarly, higher densities of young (age-0 and age-1) red snapper were shown to inhabit increasing complex reef structure (Lingo and Szedlmayer, 2006; Piko and Szedlmayer, 2007) with an absence of predators (Mudrak and Szedlmayer, 2012). At large structures, such as platforms, complexity probably is lower and the abundance of potential predators likely is higher than at the smaller artificial reefs used in our study. Therefore, these larger reefs may not support as

[3] Gitschlag, G. R., M. J. Schirripa, and J. E. Powers. 2001. Estimation of fisheries impacts due to underwater explosives used to sever and salvage oil and gas platforms in the U. S. Gulf of Mexico. OCS Study MMS 2000–087, 94 p. Final report prepared by the National Marine Fisheries Service for the U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Region, New Orleans, LA. [Available from http://www.boemre.gov/itd/abstracts/2000-087a.html.]

many red snapper per unit of volume as more complex, smaller structures. For example, an inverse relation was shown between the abundance of red snapper and the density of offshore platforms—possibly a result of greater exposure of young red snapper to predators that aggregate around such platforms (Gallaway et al., 1999). The higher densities of red snapper on the reefs found in our study indicate that these artificial reefs may provide red snapper enhanced protection from predation as well as greater overall carrying capacity.

Conclusions

The significant differences observed in ages of red snapper among artificial reefs of different ages provide support for the hypothesis that artificial reefs enhance red snapper production. Although it is obvious that red snapper are attracted to artificial reefs, especially as young new recruits, and older red snapper may show more transient behavior among reefs, it appears that many red snapper reside on particular reefs for several years and that artificial reefs may allow for higher biomass of red snapper by providing additional reef habitat. However, at some point, the number of artificial reefs placed in the northern Gulf of Mexico may surpass the region's carrying capacity and the addition of more artificial structures will no longer increase the population of red snapper. Future research that examines the carrying capacities of artificial habitats is needed and would provide information on when an overall environmental carrying capacity for red snapper has been reached. Additional fishery-independent studies throughout the northern Gulf of Mexico, with methods similar to those used in our study, would be useful for making better management decisions regarding catch limits for red snapper.

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Temporal trends (2000–2011) and influences on fishery-independent catch rates for loggerhead sea turtles (*Caretta caretta*) at an important coastal foraging region in the southeastern United States

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Abstract—Seasonal trawling was conducted randomly in coastal (depths of 4.6–17 m) waters from St. Augustine, Florida, (29.9°N) to Winyah Bay, South Carolina (33.1°N), during 2000–03, 2008–09, and 2011 to assess annual trends in the relative abundance of sea turtles. A total of 1262 loggerhead sea turtles (*Caretta caretta*) were captured in 23% (951) of 4207 sampling events. Capture rates (overall and among prevalent 5-cm size classes) were analyzed through the use of a generalized linear model with log link function for the 4097 events that had complete observations for all 25 model parameters. Final models explained 6.6% (70.1–75.0 cm minimum straight-line carapace length [SCLmin]) to 14.9% (75.1–80.0 cm SCLmin) of deviance in the data set. Sampling year, geographic subregion, and distance from shore were retained as significant terms in all final models, and these terms collectively accounted for 6.2% of overall model deviance (range: 4.5–11.7% of variance among 5-cm size classes). We retained 18 parameters only in a subset of final models: 4 as exclusively significant terms, 5 as a mixture of significant or nonsignificant terms, and 9 as exclusively nonsignificant terms. Four parameters also were dropped completely from all final models. The generalized linear model proved appropriate for monitoring trends for this data set that was laden with zero values for catches and was compiled for a globally protected species. Because we could not account for much model deviance, metrics other than those examined in our study may better explain catch variability and, once elucidated, their inclusion in the generalized linear model should improve model fits.

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Analysis of temporal trends in capture rates is a significant part of conducting stock assessments (Hilborn and Walters, 1992). Capture rates generated through fishery-independent methods are ideal; however, fishery-dependent data sets are also suitable provided that historical shifts in fishing practices are accounted for (Walters, 2003). Although the value of monitoring capture rates increases with expanded temporal scope, the temporal scope of a data set often is abbreviated by economics. Consequently, resource management decisions often rely on an assortment of observations compiled across a variety of sources. Provided that heterogeneous data sets span a gamut of time and interface well, such practices are not inherently problematic. However, vast temporal gaps or intricacies that preclude the bridging of data sets can be problematic for the assessment of long-term patterns and, ultimately, for effective resource management, particularly for long-lived species.

Sea turtles (order Testudines) are long-lived marine species that have come to represent the link between anthropogenic activities and their effects on sea turtle populations (Musick, 1999). Annual monitoring of nests and eggs has generated data sets with durations that approximate the assumed generation time for some cohorts (Troëng and Rankin, 2004; Balazs and Chaloupka, 2004; Witherington et al., 2009). Conversely, challenges associated with the collection of sea turtle data in aquatic environments have resulted in less information on abundance trends for life history stages between hatchling and adult (NRC, 2010). Despite extensive characterizations of incidental capture of sea turtles in fisheries (Wallace et al., 2010a) and subsequent evaluation of mitigation measures (Brewer et al., 1998; Gilman et al., 2006; Murray, 2011), few temporal analyses of fishery-dependent captures exist. Notable exceptions include 2 assessments (both spanning 8-year periods) of loggerhead sea turtle (*Caretta caretta*) catch from pelagic longline fisheries in the southwestern Atlantic Ocean (Pons et al., 2010) and from neritic pound-net fisheries in the northwestern (NW) Atlantic Ocean (Epperly et al., 2007). Published accounts of temporal trends in

fishery-independent catch rates that span one or more decades are also sparse, typically originate from spatially refined study locations, and are largely restricted to green (*Chelonia mydas*) and loggerhead sea turtles in the South Pacific and NW Atlantic Oceans (Limpus et al., 1992; Ehrhart et al., 2007; Arendt et al., 2012a).

In addition to limited spatial context, localized surveys also tend to be conducted in sea turtle aggregation areas where individuals exhibit site fidelity (Byles, 1988; Avens et al., 2003). Consequently, the statistical pitfalls attributed to monitoring fishery-dependent capture rates in areas of resource concentration (Hilborn and Walters, 1992) also apply, and they necessitate the introduction of an element of randomization to reduce bias. For example, Epperly et al. (2007) randomly selected pound nets for monitoring sea turtle catch rates, and Arendt et al. (2012a) systematically sampled among spatial blocks to monitor sea turtle catch rates within a shipping channel. Although such practices improve statistical design, they are not as robust as truly randomized sampling. Excluding random selection of aerial survey transects (Epperly et al., 1995a), which do not facilitate assessment of critical demographic parameters (Braun-McNeill et al., 2007), data on sea turtle relative abundance from random sampling on foraging grounds over large spatial expanses are not available globally.

To improve the random nature and spatial scope of in-water sea turtle data collected in the NW Atlantic Ocean, a trawl survey of sea turtle relative abundance was initiated in 2000 to address the need for "long-term, in-water indices of loggerhead abundance in coastal waters...to identify relative abundance of sea turtles over time, and to detect changes in size composition with implications regarding recruitment" (TEWG, 1998). Before mandated use of turtle excluder devices (TEDs), the decline of sea turtles in the NW Atlantic Ocean was attributed to the drowning of turtles during commercial shrimp trawling (NRC, 1990); therefore, sampling by trawling may seem odd as a sampling method. However, reduced tow times (Sasso and Epperly, 2006) enabled safe use of this accepted technique to capture sea turtles in turbid waters (Butler et al., 1987). For our study, we test the null hypotheses of no change in annual loggerhead capture rates in coastal waters from Winyah Bay, South Carolina, (33.1°N) to St. Augustine, Florida, (29.9°N) between 2000 and 2011 overall (objective 1) and for prevalent 5-cm size classes (objective 2). We also test the null hypothesis of no significant influence of 26 parameters on capture rates (objective 3) with a generalized linear model, the most powerful linear model (Hilborn and Walters, 1992).

Materials and methods

Sampling and data collection

For this study, sampling was conducted in coastal waters (at depths of 4.6–17.0 m) between Winyah Bay, South Carolina, and St. Augustine, Florida (Fig. 1). Four subregions were recognized on the basis of sampling strata established by the Southeastern Area Monitoring and Assessment Program (SEAMAP). The subregion that spanned from St. Augustine, Florida, to Brunswick, Georgia, for example, corresponded with sampling strata from the northern portions of SEAMAP strata 27–28 to strata 34. SEAMAP strata 35 to 40 approximated the subregion from Brunswick to Savannah, Georgia. SEAMAP strata 41 to 46 and 47 to 50 corresponded with the subregions from Savannah, Gerogia, to Charleston, South Carolina, and from Charleston to Winyah Bay, South Carolina, respectively. Sampling began in mid-May, roughly 6 weeks after the seasonal return of loggerhead sea turtles to nearshore coastal waters (Arendt et al., 2012b). Sampling concluded in late July in all years except 2000, when sampling had to be extended into mid-August because of a temporary shutdown that occurred (in July) when we reached the initially permitted sea turtle catch limits authorized by the National Marine Fisheries Service (NMFS), Office of Protected Resources.

At the start of each sampling year, a list of stations was randomly selected from a universe of 1500 coordinate pairs that represented the center of 3.4-km^2 grids of trawlable seafloor within the overall survey boundaries. Sampling was completed with 2–3 vessels, with a staggered north-to-south start, which primarily arose as a result of vessel availability. All vessels that participated in this study towed paired 18.3-m (head rope), 4-seam, 4-legged, 2-bridle nets with a net body that consisted of a 10.2-cm bar and 20.3-cm stretch mesh. Subregion sampling alternated weekly to the north or south of vessel homeports to reduce spatiotemporal bias. Aboard each vessel, the daily order of station sampling alternated haphazardly between stations located roughly <6 km from shore and stations located >6 km from shore to diversify longitudinal sampling with respect to time of day and tide stage while still enabling a large (~100 km of latitude) area to be sampled by each vessel weekly.

Captured sea turtles were removed from nets and examined for general health and injuries. In the event of unconscious sea turtles, project staff had been trained in veterinarian- and NMFS-approved resuscitation protocols that involved manual ventilation by a self-refilling valve-bag apparatus. Sea turtles were scanned for pre-existing tags; if none were found, each sea turtle was assigned a unique identification number when it was first encountered (and the number was used again to denote recapture events). A suite of morphometric measurements were collected, but, here, we report only minimum straight-line carapace length (SCLmin) measured with tree calipers. Sea turtles were tagged externally (2 Inconel 681[1] flipper tags, National Band and Tag Co., Newport, KY, purchased through the Archie Carr Center for Sea Turtle Research, Gainesville,

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

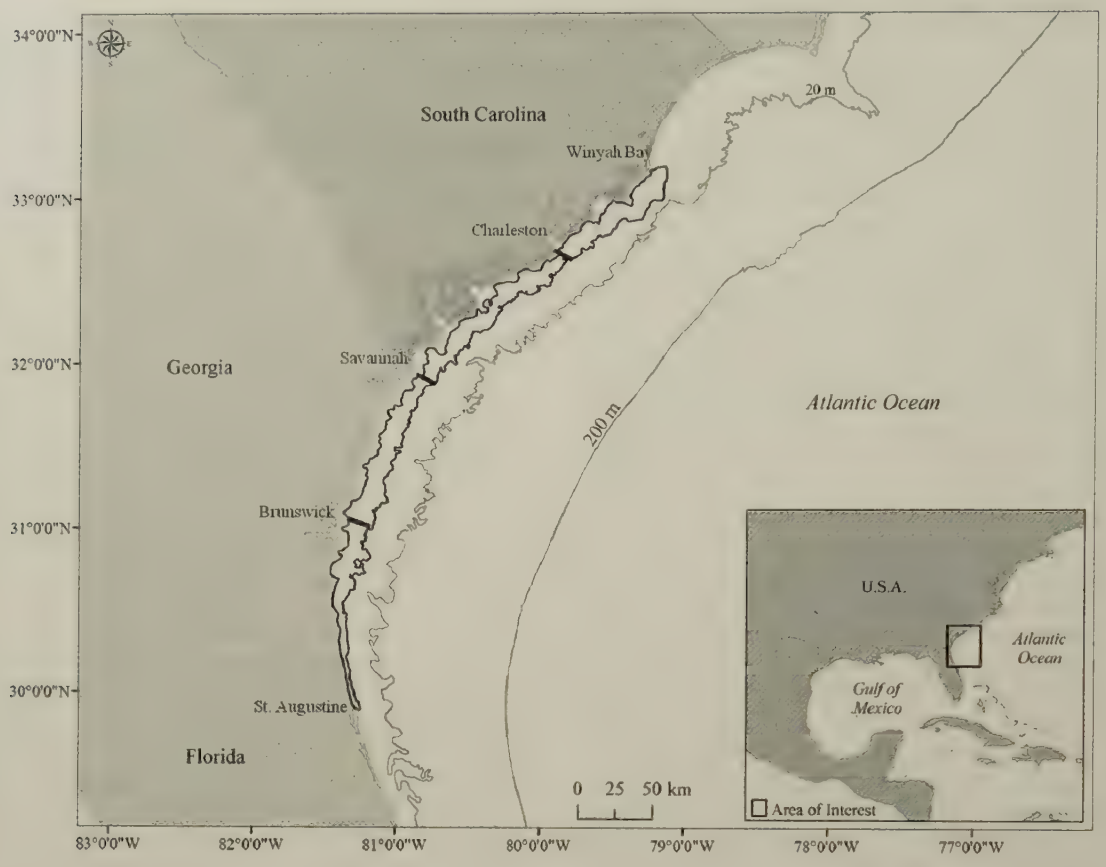

Figure 1

Map showing the location and spatial extent of the regional sea turtle trawl survey conducted in 2000–03, 2008–09, and 2011 between Winyah Bay, South Carolina, (33.1°N) and St. Augustine, Florida, (29.9°N), and the 20-m and 200-m depth contours. Thick black bars denote breaks between geographic subregions within the study area.

FL) and internally (passive integrated transponder tag TX1406L, 125 kHz, Biomark, Inc., Boise, ID) before release to assess recapture events.

Data analysis

Moran's index (ArcGIS ArcInfo Desktop, vers. 10.0; ESRI, Redlands, CA) was used to evaluate the spatial randomness of trawling events among years. Moran's index measures event similarity based on both the locations (x, y coordinates) and attribute values (year). With any set of event locations, and a single attribute, this index measures whether the location pattern is clustered, dispersed, or random on the basis of that attribute. The Moran's index value runs from +1.0 (clustering) to –1.0 (dispersion), and large or small (negative) Z scores indicate Moran's index values in the tails of the distribution and unlikely to be random.

A chi-square contingency test (significance level [α]=0.05) was performed in Minitab 15 (Minitab, Inc., State College, PA) to evaluate annual distribution among 3 types of seafloor habitat—"hard," "probably hard," and "not hard"—as determined from the co-occurrence of ≥3, 2, or ≤1 of 56 hard-bottom indicator species[2,3], respectively. Temporal trends in distribution of seafloor types were analyzed with linear regression. Sampling effort among years and subregions was also examined with chi-square analysis.

Loggerhead sea turtle catch per event (response variable) was examined with R software (vers. 2.13.0; R Development Core Team, 2011) in the context of an offset term (log of the linear distance, in kilometers, between trawl start and end locations). Catch, rather than catch rate, was analyzed given a 33% decrease in permitted bottom trawl time (and, therefore, trawl transect length) during 2008–09 relative to the other five survey

[2] Reed, J. K. 2004. General description of deep-water coral reefs of Florida, Georgia and South Carolina: A summary of current knowledge of the distribution, habitat, and associated fauna. A Report to the South Atlantic Fishery Management Council, NOAA, NMFS, 71 p

[3] VanDolah, R., P. Maier, G. Sedberry, C. Barans, F. Idris, and V. Henry. 1994. Distribution of bottom shelf habitats on the continental shelf off South Carolina and Georgia. Final Report submitted to Southeast Area Monitoring and Assessment Program South Atlantic Committee, 46 p.

years. Catch was examined annually for the overall data set and for 5-cm size classes between 40.1–45.0 cm and 100.0–105.0 cm SCLmin that had at least 100 total captured loggerhead sea turtles. For 23 turtles with posterior carapace injuries, ad hoc assignment to 5-cm size classes was made with the use of paired (SCLmin and straight-line carapace width [SCW]) measurements for loggerhead sea turtles (1230) captured in this survey. The paired measurements were used in this calculation: SCLmin=(1.42×SCW) – 10.5 (F=10,579; P<0.001; coefficient of determination [r^2]=0.90). Catch data were fitted to a negative binomial distribution and analyzed through the use of a generalized linear model with a log link function, after exclusion of 2% of attempted sampling events because of tow times (55 events) that were not ±95% of the target trawl duration (20 min in 2008–09, 30 min in all other years) or where suspect trawl start or end locations could not be resolved (42 events). Thirteen additional sampling events were excluded because data were missing for them for at least 1 of 25 model terms.

Two of the included model terms were temporal: year and time of day at the start of each trawling event (1=≤0959 h local standard time [LST]; 2=1000–1259 h; 3=1300–1559 h; 4=≥1600 h). However, two standard temporal terms (i.e., season and day of year) were not included in the model. Such temporal terms were excluded because this survey was conducted within 1 month of the summer solstice (i.e., a peak and stable photoperiod) and nearly 2 months after juvenile loggerhead sea turtles return to nearshore coastal waters in this region (Arendt et al., 2012b). Another reason for their exclusion was a spatiotemporal bias in sampling due to staggered vessel start dates.

Six spatial model terms were used. One of these parameters consisted of geographic subregions: 1=Winyah Bay to Charleston, South Carolina; 2=Charleston, South Carolina, to Savannah, Georgia; 3=Brunswick to Savannah, Georgia; 4=St. Augustine, Florida, to Brunswick, Georgia. The other spatial terms were minimum distance from shore (in kilometers) at the start of each trawling event (determined with ArcGIS ArcInfo 10.0); distance (in kilometers) and bearing (in degrees) from the closest of 31 estuary inlets within the study area; trawl transect bearing (in degrees), computed with Pythagorean theorem; and seafloor type assigned by co-occurrence of ≤1, 2, or ≥3 of 56 hard-bottom indicator species[2,3].

Six environmental parameters were measured in situ at the start of each trawling event, several of which are known to influence spatial distributions of loggerhead sea turtles in pelagic habitats (Báez et al., 2007; Mansfield et al., 2009; Kobayashi et al., 2011). Sea-surface temperature (SST, in degrees Celsius) was measured by the ship's transducer or, in 2000 and 2001, read by a digital thermometer for a bucket of surface water. Mean water depth (in meters) was recorded by a fathometer at the start and end of each trawling event, after which the relative change (in percentage) between the start and end locations was recorded. Wind velocity (in knots) and direction were recorded with a shipboard anemometer. The relative distribution of cloud cover (in percentage) across the entire dome of sky also was estimated. Wind direction was recorded as text at sea but later converted to numeric values in this manner: north (0°), north-northeast (22.5°), northeast (45°), etc. Where wind velocities were recorded as calm, wind direction was assigned to the direction recorded just before winds became calm. Hourly SST data from the buoy at Gray's Reef National Marine Sanctuary (GRNMS) (station 41008; http://www.ndbc.noaa.gov;) were used for substitutions for 539 trawling events with missing SST given ±10% agreement for 95% of 3100 paired observations from both data sets.

Seven model terms were generated through the use of external data sets and included 8-day compilations of chlorophyll-*a* (Chl-*a*, in miligrams per cubic mililiter; http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html#) at resolutions of 9 km (Sea-viewing Wide Field-of-view Sensor [SEAWIFS]; 2000–02) and 4 km (Moderate Resolution Imaging Spectroradiometer, Aqua satellite [MODIS-A]; ≥2003) for the observation closest (8.5 ±18.9 km; mean ±standard deviation [SD]) to the trawling event midpoint; daily mean and change in barometric pressure (milibars) recorded hourly at the GRNMS buoy; monthly North Atlantic Oscillation (NAO) index values from the NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml); tide stage (0=ebb, 1=flood) and range (in meters) in water level between high and low water during the tidal event when sampling was conducted, determined from hourly data at National Ocean Service gauges near Winyah Bay, South Carolina (8662245), Charleston, South Carolina (8665530), Savannah, Georgia (8665530), and Mayport, Florida (8670870); and random scrambling of event order (H_6=2.64, P=0.852 by year) to evaluate the model (Kobayashi et al., 2011). In addition to the model and offset terms described above, null models also contained up to 4 interaction terms (mean depth vs. distance from shore; mean depth vs. distance from inlet; distance from inlet vs. distance from shore; year vs. NAO index) identified with a correlation test (Pearson's coefficient of correlation [r]>0.4) performed in R. As such, terms in the null model were analyzed in the following order: Loggerhead count=year + NAO + (*year*NAO*) + subregion + time of day + mean depth + distance from shore + trawl depth change + distance from inlet + (*mean depth*distance from shore*) + (*mean depth*distance from inlet*) + (*distance from shore*distance from inlet*) + bottom type + cloud cover + wind velocity + wind direction + daily mean barometric pressure + interdaily change in daily mean barometric pressure + bearing from inlet + tide stage + tide range + transect bearing + Chl-*a* + SST + random order + log(transect length).

Final model selection was accomplished through stepwise regression based on the lowest Akaike's information criterion (AIC) score. A chi-square analysis of deviance was performed in R to assess the statistical significance of variables retained in the final model.

Table 1

Temporal distribution of sampling effort (number of events), loggerhead sea turtle (*Caretta caretta*) captures (no. of Cc) and recaptures (by recapture year) in the sea turtle trawl survey conducted in 2000–03, 2008–09, and 2011 in a coastal foraging region in the southeastern United States.

Year	Number of events	Tagged no. of Cc	Recaptured							
			2000	2001	2002	2003	2008	2009	2011	Total
2000	621	172	0	0	1	4	0	0	0	5
2001	603	177		0	0	2	1	2	0	5
2002	684	209			1	1	0	0	2	4
2003	714	250				0	0	0	0	0
2008	589	167					0	0	0	0
2009	586	152						0	1	1
2011	410	135							1	1
Total	4207	1262	0	0	2	7	1	2	4	16

Quantile residuals (Dunn and Smyth, 1996) were then plotted against each variable to assess trends and model-assigned statistical significance of variables. Cumulative deviance attributed to all final model parameters was expressed as a percentage of null deviance to characterize the extent to which the final model accounted for catch variation. Linear regression was used to assess model fits (AIC vs. counts and SD) and annual mean modeled catch of loggerhead sea turtles. Confidence intervals ([CI], 95%) around mean catch were computed with *t*-statistics from Table B3 in Zar (1996).

Results

Sampling effort and catch distribution

Random sampling (Moran's Index=0.00, *Z*-score=0.67, P=0.501) was attempted for 4207 trawling events during 7 sampling years between 2000 and 2011. Of 1262 captured loggerhead sea turtles, 16 were captured twice during this survey (Table 1) up to 9 years later (mean ±SD=3.9 ±3.2 years). Two loggerhead sea turtles tagged during this study were recaptured by other programs (after 0.3 and 1.9 years), and 14 loggerhead sea turtles tagged by other programs (3.4 ±3.4 years earlier) also were captured in this study. No loggerhead sea turtles died during this study, and only 3 turtles required resuscitation. Six loggerhead sea turtles tagged and released in this study were subsequently (3.0 ±1.8 years later) reported as stranded dead, 5 of them on beaches adjacent to the survey area and the sixth one in the northern Gulf of Mexico.

Sampling effort was significantly different among years and subregions (χ^2_{18}=455, P<0.001). Greatest annual sampling effort occurred in 2002–03 (343–355 h; 18–19% of total) followed by 2000–01 (300–309 h; 16% of total) and then 2008–11 (194–204 h; 10–11% of total). The greatest amount of sampling effort was expended between Brunswick and Savannah, Georgia, (533 h; 28% of total), followed by Savannah, Georgia, to Charleston, South Carolina, (501 h; 26% of total), St. Augustine, Florida, to Brunswick, Georgia, (465 h; 24% of total), and Charleston to Winyah Bay, South Carolina, (404 h; 22% of total).

Loggerhead sea turtles were captured in 23% (951) of sampling events, with up to 7 individual loggerhead sea turtles captured in one sampling event. A single loggerhead sea turtle was the most common positive catch observed and accounted for 20% of sampling events in 2011 (83 of 410) to 15% of sampling events in 2009 (87 of 586); however, the ratio of zero- to single-catch events was not significantly different among years (χ^2_6=7.5, P=0.275). Double catch of loggerhead sea turtles occurred in 4% (185) of sampling events and was not significantly different among years (χ^2_6=3.1, P=0.800). Three or more loggerhead sea turtles were captured only in 1% (46) of attempted sampling events between 2000 and 2011.

Model fits

Catch rate trends were analyzed for 1227 loggerhead sea turtles captured in 4097 sampling events with complete effort and companion data. Final model AIC scores ranged from 951.0 (75.1–80.0cm SCLmin) to 5550.1 (overall; Table 2). The count of sampling events with zero turtle catches, both overall and for each of 5 prevalent 5-cm size classes, was significantly and positively associated with final model AIC ($F_{1,4}$=1123.6, r^2=1.00, P<0.001) and SD ($F_{1,4}$=1010.5, r^2=1.00, P<0.001). The overall final model explained 8.4% of deviance in the overall data set, with between 6.6% and 14.9% of deviance explained for prevalent 5-cm size classes (Table 2). In the final overall model, 12 of 25 parameters (48%) were retained, with between 6 (24%) and 12 (48%) parameters retained in the final model for prevalent 5-cm size classes (Table 3). Among parameters retained in final models, only 50% (3 of 6) to 67% (8 of 12) were deemed significant (Table 3).

Table 2

Assessment of generalized linear model fits for loggerhead sea turtle (*Caretta caretta*) catch overall and with respect to prevalent 5-cm size classes of minimum straight-line carapace length. Best model fits (12.2–14.9% of model deviance explained) were associated with the smallest and largest size classes examined, with half as much model deviance generally explained for intermediate size classes.

Model metric	Overall	55.1–60.0	60.1–65.0	65.1–70.0	70.1–75.0	75.1–80.0
AIC score, null model	5573.2	1080.7	2033.2	2285.8	1831.1	966.0
AIC score, final model	5550.1	1052.1	2004.0	2258.7	1805.5	951.0
Null model deviance	3080.8	793.6	1407.1	1514.7	1325.4	757.4
Final model deviance	2822.3	697.2	1248.8	1403.3	1238.2	644.4
Percentage of deviance explained	8.4	12.2	11.3	7.4	6.6	14.9

Catch rate influences

Geographic subregion, distance from shore, and sampling year were the only parameters retained as significant terms in all final models (Table 3). Geographic subregion was the most important parameter overall (3.9% of deviance) but was the most important observed influence on catch rates for loggerhead sea turtles that measured ≤70.0cm SCLmin, where it accounted for 3.2–7.6% of data set deviance (Table 3). Catch increased significantly ($F_{1,2}$=27.3, r^2=0.90, P=0.035; Fig. 2) between the subregion of Winyah Bay to Charleston, South Carolina, (mean ±95% CI=0.174 ±0.003 turtles per km; CV=0.24) and the subregion of Brunswick, Georgia, to St. Augustine, Florida, (0.468 ±0.013 turtles per km; CV=0.44).

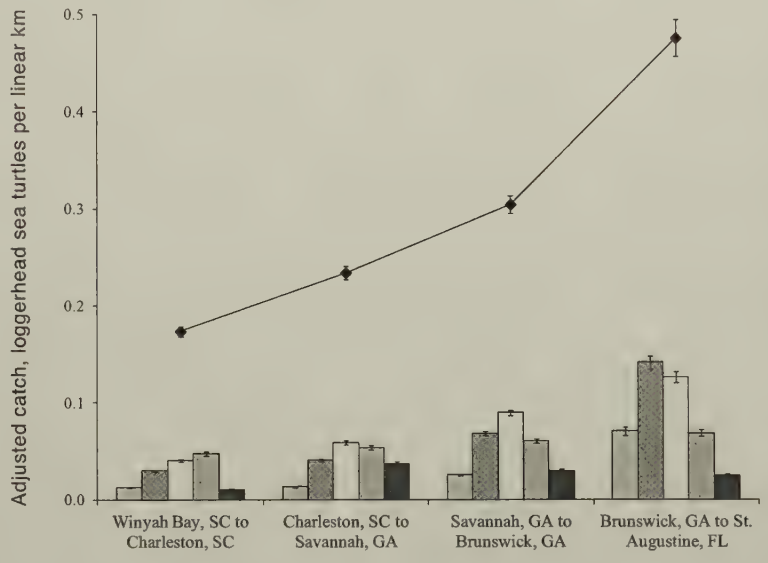

Figure 2

Spatial variability in modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer for 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–03, 2008–09, and 2011. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

Distance from shore accounted for 1.5% of data set deviance overall, but between 0.1% and 2.5% of data set deviance among 5-cm size classes (Table 3). Catch rates decreased systematically with distance from shore (Fig. 3), with overall trends driven largely by loggerhead sea turtles that measured 60.1–70.0 cm SCLmin and captured within 5 km from shore.

Sampling year explained 0.8% of data set deviance overall and between 1.0–6.1% of data set deviance among 5-cm size classes (Table 3). Annual catch rates (sea turtles per linear kilometer) ranged from 0.256 ±0.014 (mean ±95%CI) in 2009 to 0.356 ±0.019 in 2003, but rates were not significantly different among years ($F_{1,5}$=0.0, r^2=0.00, P=0.944). Interannual differences in mean catch rates for loggerhead sea turtles that measured 55.1–75.0 cm SCLmin (Fig. 4, A and B) were not significantly different ($F_{1,5}$=0.5–4.1, r^2=0.00–0.34, P=0.098–0.500). Catch rates for loggerhead sea turtles 75.1–80.0 cm SCLmin (Fig. 4B) increased significantly ($F_{1,5}$=24.1, r^2=0.79, P=0.004) between 2000 (4, 2% of captures; CV=0.86) and 2011 (25, 19% of captures; CV=0.92).

Four terms were retained only as significant terms for a subset of all final models. The interaction between mean water depth and distance from the closest inlet was retained as a significant model term in all final models, except for the smallest (55.1–60.0 cm SCLmin) and largest (75.1–80.0 cm SCLmin) size classes evaluated, but accounted for ≤0.7% of data set deviance (Table 3). Time of day and the interaction between sampling year and the NAO index was retained as signifi-

Table 3

The influence of model terms on counts (dependent variable) of loggerhead sea turtles (*Caretta caretta*) per trawling event (offset=log[*trawl transect length*]) in the sea turtle trawl survey in a coastal foraging region in the southeastern United States. *P*-values (*=significant; chi-square) are provided for the overall data set and prevalent 5-cm size classes. The percentage (%) of explained model deviance attributed to terms retained in the final model is provided.

Model term	Overall	%	55.1–60.0	%	60.1–65.0	%	65.1–70.0	%	70.1–75.0	%	75.1 –80.0	%
Year	<0.001*	0.8	0.036*	1.7	0.798	0.2	0.022*	1.0	<0.001*	3.4	<0.001*	6.1
North Atlantic Oscillation	—	—	—	—	—	—	—	—	—	—	0.674	0.0
Year × North Atlantic Oscillation	—	—	—	—	—	—	—	—	—	—	0.018*	2.0
Subregion	<0.001*	3.9	<0.001*	7.6	<0.001*	6.3	<0.001*	3.2	0.020*	0.7	0.002*	1.9
Time of day	—	—	—	—	—	—	—	—	—	—	0.024*	1.3
Mean trawl depth	0.973	0.0	—	—	0.192	0.1	0.394	0.1	0.362	0.1	0.007*	1.0
Trawl depth change	—	—	—	—	0.129	0.2	—	—	—	—	—	—
Distance from shore	<0.001*	1.5	<0.001*	2.4	<0.001*	2.5	0.001*	0.7	0.026*	0.4	0.428	0.1
Distance from inlet	0.270	0.0	0.117	0.3	0.527	0.0	0.407	0.0	0.092	0.2	—	—
Mean depth × distance from shore	—	—	—	—	—	—	—	—	—	—	0.076	0.4
Mean depth × distance from inlet	<0.001*	0.4	—	—	0.005*	0.6	0.001*	0.7	0.003*	0.7	—	—
Distance: from shore *x* inlet	0.020*	0.2	—	—	—	—	0.196	0.1	—	—	—	—
Seafloor habitat type	<0.001*	0.8	—	—	0.013*	0.6	<0.001*	1.6	0.135	0.3	0.060	0.7
Cloud cover	0.113	0.1	—	—	—	—	—	—	0.123	0.2	—	—
Wind speed	—	—	—	—	—	—	—	—	—	—	0.114	0.3
Wind direction	—	—	—	—	0.134	0.2	—	—	—	—	—	—
Mean daily barometric pressure	—	—	—	—	—	—	—	—	—	—	—	—
Daily change in barometric pressure	—	—	—	—	—	—	—	—	—	—	—	—
Bearing from inlet	<0.001*	0.4	—	—	0.047*	0.3	—	—	0.003*	0.6	0.268	0.2
Tide stage	—	—	—	—	—	—	—	—	—	—	—	—
Tide range	—	—	0.699	0.0	—	—	—	—	—	—	0.008*	0.9
Transect bearing	0.021*	0.2	—	—	0.036*	0.3	—	—	—	—	—	—
Chlorophyll-*a*	—	—	0.216	0.2	—	—	—	—	—	—	—	—
Sea-surface temperature	0.205	0.1	—	—	—	—	—	—	—	—	—	—
Random ordering	—	—	—	—	—	—	—	—	—	—	—	—

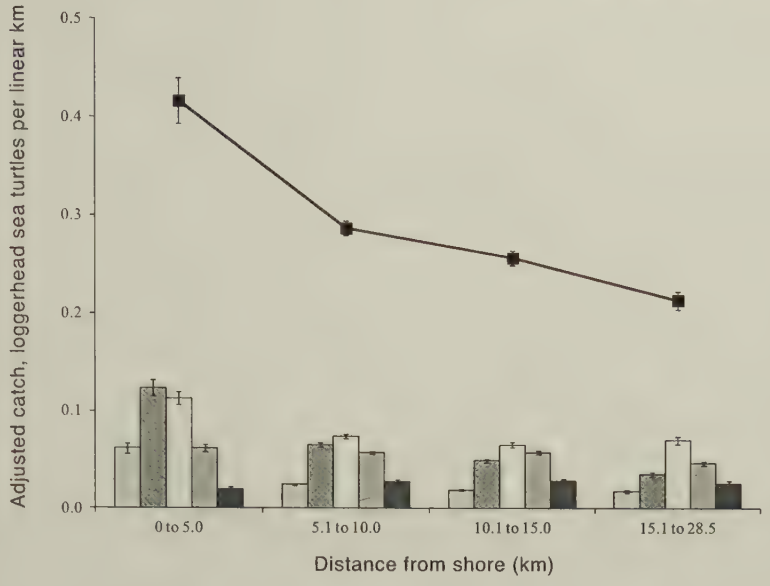

Figure 3

Modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer with respect to incremental distances from shore during 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–03, 2008–09, and 2011. Distance from shore was analyzed as a continuous variable, but it is plotted here as a factor for comparative purposes. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

cant terms in the final model for loggerhead sea turtles 75.1–80.0 cm SCLmin and accounted for 1.3% and 2% of data set deviance, respectively (Table 3). Transect bearing was retained only as a significant model term overall and for loggerhead sea turtles that measured 60.1–65.0 cm SCLmin and accounted for ≤0.3% of data set deviance.

Seafloor type, bearing from inlet, tide range, mean trawl depth, and the interaction between distance from shore and distance from inlet were retained as a mixture of significant or nonsignificant terms in a subset of final models. Seafloor type was significant for the overall data set and for loggerhead sea turtles that measured 60.1–70.0 cm SCLmin, where it explained 0.6–1.6% of data set deviance (Table 3). Greatest catch rates were associated with habitats that were not classified as hard (Fig. 5), and these habitats represented 54 ±9% (mean ±SD) of all trawling events; probably hard and hard habitats constituted 21 ±5% and 25 ±8% of trawling events, respectively. Distributions of seafloor type differed significantly among years (χ^2_{12}=160.0, P<0.001); however, temporal trends were not detected ($F_{1,5}$=0.0, r^2=0.00, P=0.966) in the annual proportion of trawling events classified as not hard.

When retained, bearing from inlet was predominantly (3 of 4 models) significant but only accounted for 0.2–0.6% of data set deviance (Table 3). Mean trawl depth and tide range were retained only as significant terms for loggerhead sea turtles that measured 75.1–80.0 cm SCLmin, where they accounted for 1.0% and 0.9% of data set deviance, respectively (Table 3). The interaction between distance from shore and distance to inlet was significant only for the overall data set in the final model, and it accounted for 0.2% of data set deviance (Table 3). Of the remaining 13 parameters, 9 were retained only as nonsignificant terms in a subset of final models and 4 were excluded from all final models (Table 3).

Discussion

Trawling generated a large annual sample size of loggerhead sea turtles over a vast coastal expanse in a concise time frame, and this large sample size in turn enabled a reliable assessment of interannual trends. Although trawling admittedly is more expensive than other methods (Bjorndal and Bolten, 2000), it is also an effective and appropriate means for the capture of sea turtles in turbid coastal waters where sea turtles are seasonally abundant (Schmid, 1995; Casale et al., 2004). Therefore, the expense associated with collection of the

data necessary to conduct stock assessments, a feat that is not possible by monitoring annual nest counts alone (Chaloupka and Limpus, 2001), is arguably an intelligent investment in the management and recovery of long-lived species. In addition to monitoring catch rates, in-water capture methods, such as trawling, enable the collection of demographic data (Roberts et al., 2005) and health assessments (Deem et al., 2009; O'Connell et al., 2010). Although such data may also be obtained from stranded animals (Monzón-Argüello et al., 2009), the opportunistic nature and reporting of stranded animals (NRC, 1990) render those data, unlike data from in-water captures, inappropriate for assessment of relative abundance trends.

A significant interannual catch trend was detected only for loggerhead sea turtles that measured 75.1–80.0 cm SCLmin, a size class that represented just 2% of loggerhead captures in 2000 but that was observed nearly 10 times as often in 2011. This size class is slightly smaller than the size at which loggerhead sea turtles reach sexual maturity in the NW Atlantic (~82 cm SCL; TEWG, 2009); therefore, increased catch rates for this size class through 2011 may not reflect mature individuals that had returned to their region of natal origin (Bowen et al., 2004). Alternatively, increased catch rates for loggerheads in this size class likely stemmed from growth of resident individuals (Mansfield et al., 2009; Arendt et al., 2012b) hatched in strong nesting years. Braun-McNeill et al. (2008) estimated that it took 17.4 years for loggerheads in the NW Atlantic to grow from 50 to 80 cm SCL, the size range associated with prevalent size classes in our study. Assuming neritic recruitment at age 11 (Conant et al., 2009) and ~50 cm SCLmin (Bjorndal et al., 2003) plus another 17.4 years (Braun-McNeill et al., 2008) to reach 80.0 cm SCL, loggerhead sea turtles of 75.1–80.0 cm SCLmin captured in 2000 likely hatched in the mid-1970s versus the mid- to late 1980s for loggerhead sea turtles in this size class captured in 2011. Given increased nest counts recorded through the 1980s (Witherington et al., 2009), increased conservation efforts in the past 3 decades, and, notably, large openings of TEDs since 2003 (Federal Register, 2003), a cohort-biased explanation seems plausible.

Stable catch rates in this study for loggerhead sea turtles that measured 55.1–75.0 cm SCLmin indicate that catch rates for loggerhead sea turtles 75.1–80.0 cm SCLmin are not likely to decline in the near term, with the assumption that high annual survival rates will continue and that catch rates observed in this study are indicative of regionwide trends. However, we also anticipate a substantial reduction in the relative abundance of the smallest loggerhead sea turtles between 2009 and 2017, consistent with a 41% decline in nest counts between 1998 and 2007 (Witherington et al., 2009) and assuming a neritic recruitment of age 11. Because a future decline in catch rates for the smallest turtles should eventually reshape future foraging ground demographic distributions, size-based monitoring is imperative. A nonsignificant decline in catch rates for loggerhead sea turtles that measured 55.1–60.0 cm SCLmin was noted between 2000 and 2003.

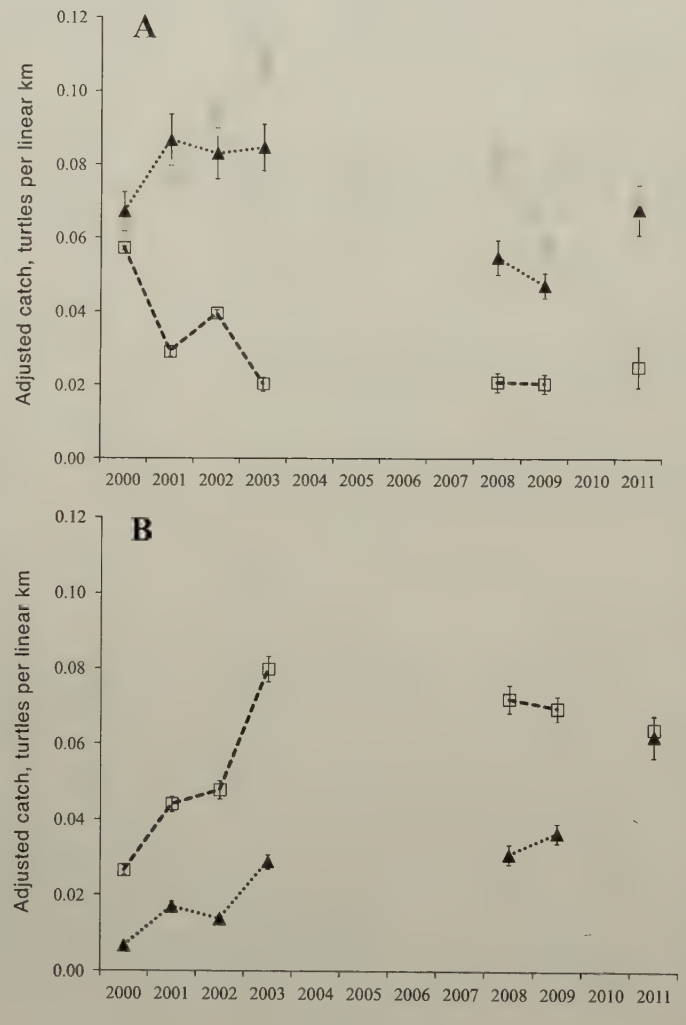

Figure 4

Annual variability in modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer among 5 prevalent size classes recorded in a sea turtle trawl survey conducted between 2000 and 2011 in a coastal foraging region in the southeastern United States. (**A**) Interannual trends for sea turtles with minimum straight-line carapace lengths (SCLmin) ≤70.0 cm were not significantly different ($P>0.05$) for turtles 55.1–60.0 cm SCLmin (squares), 60.1–65.0 cm SCLmin (triangles), or 65.1–70.0 cm (circles). (**B**) Interannual trends for the largest loggerhead sea turtles were not significantly different ($P>0.05$) for turtles 70.1–75.0 cm SCLmin (squares) but were significantly different ($P=0.004$) for turtles 75.1–80.0 cm SCLmin (triangles).

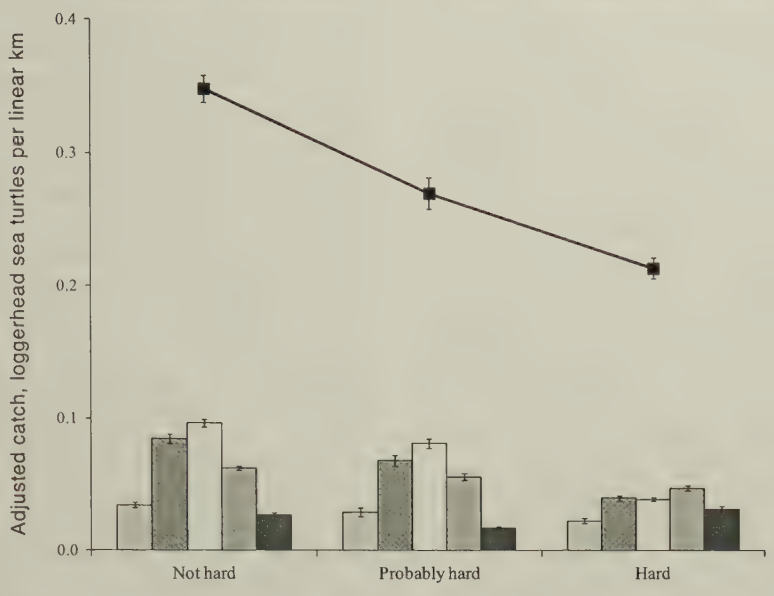

Figure 5

Modeled catch (mean ±95% CI) of loggerhead sea turtles (*Caretta caretta*) per linear kilometer with respect to type of seafloor habitat during 4097 coastal trawling events conducted between St. Augustine, Florida, (29.9°N) and Winyah Bay, South Carolina, (33.1°N) in 2000–2003, 2008–2009, and 2011. Seafloor type was classified as "hard" if ≥3 co-occurring indicator species were collected during the trawling event but classified as "probably hard" if only 1 or 2 indicator species were collected. The black line denotes overall catch rates. Bars denote the following 5-cm size classes of minimum straight-line carapace length: 55.1–60.0 (light gray); 60.1–65.0 (dark gray); 65.1–70.0 (white); 70.1–75.0 (medium gray); 75.1–80.0 (charcoal).

However, atypically high catch rates for this size class in 2000 were attributed to strong Gulf Stream intrusion across the continental shelf (evidenced by large mats of the brown macroalgae *Sargassum* and "tar ball" deposits on South Carolina beaches; senior author, pers. observ.). Between 2003 and 2011, catch rates for this size class remained relatively stable; therefore, although we remain hopeful that this trend will persist, we urge attentive monitoring of catch rates for this size class as a high priority throughout the region through at least 2017.

Even stable catch rates between 2000 and 2011 are encouraging for recovery of this species. Standardized catch rates (i.e., turtles per 30.5 net-hour) calculated by Maier et al.[4] for this study in 2003 (the year of the highest catch rates in this study) were 40 times greater than catch rates in coastal surveys in the South Atlantic Bight (SAB) from 1950 to 1976 (Bullis and Drummond, 1978) and 13 times more than rates reported for the SAB shrimp fishery in the 1970s (Henwood and Stuntz, 1987). Although historical data sets were collected by fishery-dependent means versus fishery-independent means in this study, the magnitude of increases cannot solely be explained by subtle differences in sampling gears or designs. Increased catch of loggerhead sea turtles also is reported elsewhere in this region (Ehrhart et al., 2007; Epperly et al., 2007; Arendt et al., 2012a), affirming historic increases in regional relative abundance of loggerhead sea turtles.

The inability to detect a significant overall trend generated over a span of more than a decade illustrates the long-term commitment needed to assess relative abundance trends for long-lived species, as well as the importance of size-based assessments of such trends. The inability to detect significant trends also reflects autocorrelated increases in variance and catch rates. As the ratio of catch to noncatch changes significantly in a data set laden with zero values, data set variance also increases, thereby confounding the ability to detect trends, unless catch rates decrease with time. This relationship also occurs independently of whether catch rates increase as a result of true increases in popula-

[4] Maier, P. P., A. L. Segars, M. D. Arendt, J. D. Whitaker, B. W. Stender, L. Parker, R. Vendetti, D. W. Owens, J. Quattro, and S. R. Murphy. 2004. Development of an index of sea turtle abundance based upon in-water sampling with trawl gear. Final Project Report to the National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, grant no. NA07FL0499, 86 p.

tion abundance or simply from aggregation of turtles in an area at the time of sampling. Nevertheless, because in-water studies can provide more temporally refined indications of pending nesting recruitment than nesting beach surveys alone, we encourage further in-water studies. As evidenced by this study and those published by Epperly et al. (2007), Pons et al. (2010), and Murray (2011), even zero-rich data sets (for which, currently, there are no alternatives for in-water sea turtle data), when analyzed with the appropriate statistical technique (Maunder and Punt, 2004), are valuable for assessments of temporal trends. This approach implies, of course, that the trend attributes can be adequately explained and that high zero catches do not reflect poor survey design.

Despite consistency in model terms affiliated with model deviance, very little model deviance was actually explained. The modest amount of model deviance explained likely stemmed from random sampling conducted in an open marine system where juvenile loggerhead sea turtles may not be randomly distributed. Specifically, nonrandom distribution is suggested by site fidelity documented by telemetry studies in estuarine (Byles, 1988; Morreale, 1999; Avens et al., 2003; Mansfield et al., 2009) and coastal (Renaud and Carpenter, 1994; Arendt et al., 2012b) habitats. Habitat preferences would seem a likely explanation for nonrandom distributions, particularly given the suggestion by Hopkins-Murphy et al. (2003) that loggerhead sea turtles associate with dense, live-bottom habitats. Unfortunately, dense, live-bottom habitats are not conducive to trawling operations and, as such, these habitats were avoided where possible in this study. Furthermore, use of large-mesh trawl webbing and mud rollers on the trawl foot rope was included to minimize the collection of sponges and gorgonians whose collection is needed to distinguish probably hard and hard habitats from not hard habitats. Nevertheless, nearly half of sampling events occurred where habitats were characterized as probably hard or hard, and, in contrast to the suggestion by Hopkins-Murphy et al. (2003), catch rates from these sampling events were significantly more reduced than rates from not hard habitats. Seafloor type was either excluded or retained as a nonsignificant term in half of the final models. However, in the absence of data on gear efficiency and performance in these different habitats, it is not possible to rule out the importance of habitat features on spatial distribution patterns at this time.

Four model parameters (geographic subregion, distance from shore, seafloor type, and year) consistently accounted for at least two-thirds (and upwards to 97%) of explained model deviance, and different contributions were associated with each parameter among the various size classes examined. In pelagic habitats, environmental parameters, such as temperature, Chl-*a*, and mesoscale eddies, influence the spatial distribution of loggerhead sea turtles (Mansfield et al., 2009; Kobayashi et al., 2011). However, SST and Chl-*a* each were retained only as a nonsignificant term in just one final model in this study. This observation is in line with localized distribution patterns reported by Arendt et al. (2012b), an outcome that would have been expected to be more variable if spatial distributions fluctuated in response to fine-scale hydrographic changes. Hydrographic conditions can create density gradients that are known to greatly influence loggerhead sea turtle distributions in the winter (Epperly et al., 1995b) but are less likely to occur during the 2 months surrounding the summer solstice, as well as where this study was conducted. As noted by Atkinson et al. (1983), "The large heat capacity of water insures a highly damped response to daily air temperature cycles, but cycles at seasonal and inter-annual time scales have a large effect. Similar arguments apply to the inner shelf salinity field, which is controlled by seasonal and inter-annual cycles of river discharge." Accordingly, when coupled with prevalent southwesterly winds, excessive freshwater runoff in spring 2003 set up a coastwide cold-water upwelling event (see discussion in Maier et al.[4]). Concurrent with altered circulation patterns, the greatest number of captures (and recaptures) of loggerhead sea turtles occurred in 2003.

Conclusions

This study is the first to report on coastal loggerhead sea turtle catch rates in a large and central portion of one of the most important foraging grounds for this species in the NW Atlantic basin (Bowen et al., 2004). Our inability to detect a significant trend among annual catch likely was the result of the short duration of our study relative to the life history of this species, and simultaneous increases in variance concurrent with increased catch rates. Stable to increasing catch for loggerhead sea turtles that corresponds with maturing or mature individuals is encouraging for continued recovery of this threatened species in the NW Atlantic, a population that fares better than most populations of this globally distributed species (Wallace et al., 2010b). Regionally, the data presented herein begin to address one of 3 demographic recovery criteria that stipulate that increases in the in-water abundance of juvenile sea turtles must occur throughout a network of monitoring sites for at least one generation (NMFS and USFWS, 2008).

Analysis of trawl data previously has received mixed reviews (Bjorndal and Bolten, 2000), primarily because of nuances specific to data sets (e.g., a single fishery-dependent data set collected at a single location after perceived historic stock decimation). The randomized sampling design employed in this study minimized temporal and spatial bias and maximized temporal and spatial coverage. Randomized sampling design increased the probability that observed catch was proportional to actual abundance, rather than hyperstable, which could have resulted from intensely sampling areas of high abundance (Hilborn and Walters, 1992). Given that a wide range of sea turtle sizes were captured, we also do not suspect that data reported herein represent a hyperdepleted scenario, where only a portion of the pop-

ulation is vulnerable to capture (Hilborn and Walters, 1992). As such, the data presented herein support the use of trawl survey data to assess abundance trends for sea turtles, at least in habitats where potential damage to the seafloor or to the sampling gear itself does not preclude the use of such surveys. In areas where dense, live bottom occurs, alternative sampling methods would be required; within the geographic region associated with this study, such alternative methods could include visually sampled transects, given increased distribution of live-bottom habitats farther from shore (Van Dolah et al.[3]) where underwater visibility is improved.

Provided that sea turtle capture rates are expressed relative to a standardized and robust effort term (such as linear kilometer used in this study), comparisons among habitats and sampling methods should still be valid. Furthermore, given the large size distribution of loggerhead sea turtles captured in this study, where dense live bottom was not routinely sampled, evaluation of size-based habitat preferences is a salient management need. We, therefore, recommend that the data collection and analytical techniques presented herein be expanded to foraging grounds conducive to trawling across geographically diverse areas. This action would allow the most complete data on in-water catch to be considered with nest trend data, and in turn would promote comprehensive decision-making regarding the management of protected sea turtle species in neritic habitats.

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